PLANT SUCCESSION AND INDICATORS

A Definitive Edition of Plant Succession and Plant Indicators

BY

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PREFACE

This is a combined and condensed edition of "Plant Succession" and "Plant Indicators," published by the Carnegie Institution of Washington in 1916 and 1920 respectively, and embodying the results of researches carried out under its auspices. The original editions having been exhausted, the Carnegie Institution has granted permission to the author to undertake the present publication but without responsibility on the part of the Institution. The two books were designed to be companion volumes, the one dealing with the concepts and principles, the other with the applications of the developmental method. In consequence, it seems entirely appropriate to combine them in a single volume, with a corresponding gain in convenience and economy. The expense of a new edition of each book has appeared prohibitive when the requirements of investigators are kept in mind, and hence every effort has been made to keep costs at the minimum without the sacrifice of essentials. It has been regarded as a scientific duty to meet the growing demand during the years the books have been out of print, as well as to render them available in supplying the background for the books mentioned below.

It has been necessary to disregard the large amount of new material as well as to omit considerable portions of the text in order to bring the two books within the compass of one volume. The comprehensive nature of the treatments makes it possible to do this without serious harm to the main themes, and especially since the portions omitted are to be expanded into as many collateral books with a full account of the researches since 1914. Thus, chapters X and XI, dealing with the studies of succession in North America and Eurasia, and chapters XII, XIII, and XIV, treating of the new field of paleo-ecology, have been omitted from "Plant Succession," while chapter IV, containing an account of the climax formations of western North America, has been left out of "Plant Indicators." Materially expanded in scope and detail, these respective portions furnish the themes for as many books, now well advanced in preparation. The chapters that constitute the main body of the two treatises have been reprinted essentially intact. The plates and text figures have necessarily been reduced by the omission of the several chapters, and reasons of economy have led to a further reduction.

Closely correlated with this series is the second volume of "Climatic Cycles and Tree Growth" by Douglass, which has just come from the press, and two related books, one devoted to a consideration of rainfall cycles, the other to an account of the cyclic changes of climate and vegetation since the Pleistocene. During the decade just passed the functions of the community have been treated in outline in "Experimental Vegetation," and this study has been carried much further in "Plant Competition," which is on the eve of publication. With these are intimately associated the four books on root develop-

ment and behavior by Weaver and his colleagues (1919, 1920, 1922, 1924), while the factors of the habitat have been the theme of "Aeration and Air-Content" (1921) and "The Phytometer Method" (1924). All these and the projects related to them have been summarized each year in the Year Book of the Carnegie Institution and the annual report of Ecological Research, reprinted from it.

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AN ANALYSIS OF THE DEVELOPMENT OF VEGETATION

AN ABRIDGMENT OF PUBLICATION NO. 242

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I. CONCEPT AND CAUSES OF SUCCESSION.

The formation an organism.—The developmental study of vegetation necessarily rests upon the assumption that the unit or climax formation is an organic entity (Research Methods, 199). As an organism the formation arises, grows, matures, and dies. Its response to the habitat is shown in processes or functions and in structures which are the record as well as the result of these functions. Furthermore, each climax formation is able to reproduce itself, repeating with essential fidelity the stages of its development. The life-history of a formation is a complex but definite process, comparable in its chief features with the life-history of an individual plant.

Universal occurrence of succession.—Succession is the universal process of formation development. It has occurred again and again in the history of every climax formation, and must recur whenever proper conditions arise. No climax area lacks frequent evidence of succession, and the greater number present it in bewildering abundance. The evidence is most obvious in active physiographic areas, dunes, strands, lakes, flood-plains, bad lands, etc., and in areas disturbed by man. But the most stable association is never in complete equilibrium, nor is it free from disturbed areas in which secondary succession is evident. An outcrop of rock, a projecting boulder, a change in soil or in exposure, an increase or decrease in the water-content or the light intensity, a rabbit-burrow, an ant-heap, the furrow of a plow, or the tracks worn by wheels, all these and many others initiate successions, often short and minute, but always significant. Even where the final community seems most homogeneous and its factors uniform, quantitative study by quadrat and instrument reveals a swing of population and a variation in the controlling factors. Invisible as these are to the ordinary observer, they are often very considerable, and in all cases are essentially materials for the study of succession. In consequence, a floristic or physiognomic study of an association, especially in a restricted area, can furnish no trustworthy conclusions as to the prevalence of succession. The latter can be determined only by investigation which is intensive in method and extensive in scope.

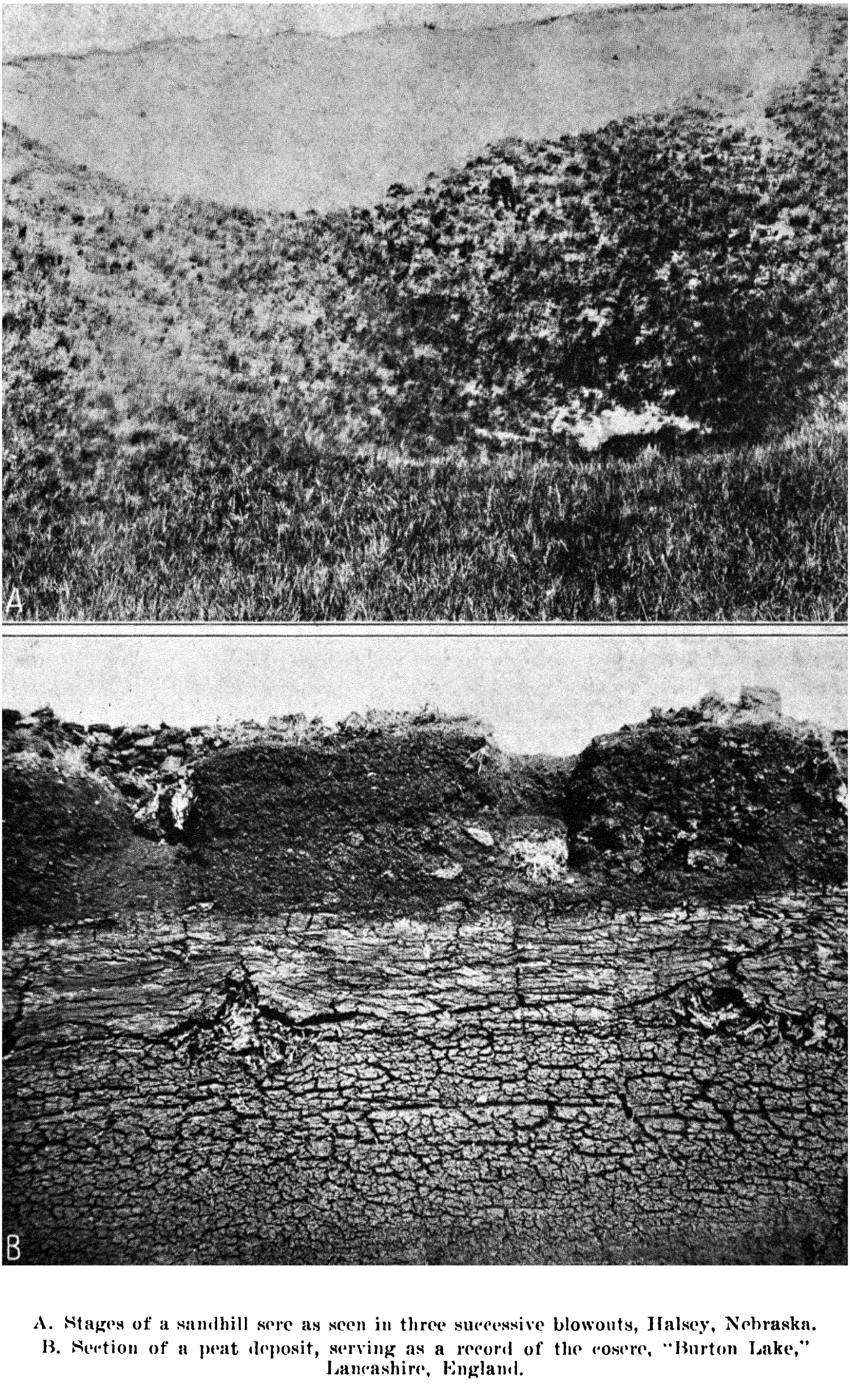
Viewpoints of succession.—A complete understanding of succession is possible only from the consideration of various viewpoints. Its most striking feature lies in the movement of populations, the waves of invasion, which rise and fall through the habitat from initiation to climax. These are marked by a corresponding progression of vegetation forms or phyads, from lichens and mosses to the final trees. On the physical side, the fundamental view is that which deals with the forces which initiate succession and the reactions which maintain it. This leads to the consideration of the responsive processes or functions which characterize the development, and the resulting structures, communities, zones, alternes, and layers. Finally, all of these viewpoints are summed up in that which regards succession as the growth or development

and the reproduction of a complex organism. In this larger aspect succession includes both the ontogeny and the phylogeny of climax formations.

Succession and sere.—In the thorough analysis of succession it becomes evident that the use of the term in both a concrete and an abstract sense tends to inexactness and uncertainty. With the recognition of new kinds of succession it seems desirable to restrict the word more and more to the phenomenon itself and to employ a new term for concrete examples of it. In consequence, a word has been sought which would be significant, short, euphonic, and easy of combination. These advantages are combined in the word *sere,* from a root common to both Latin and Greek, and hence permitting ready composition in either. The root *ser-* shows its meaning in Latin *sero,* join, connect; *sertum,* wreath; *series,* joining or binding together, hence sequence, course, succession, lineage. In Greek, it occurs in *εἴρω,* to fasten together in a row, and in *σειρά, σηρά,* rope, band, line, lineage. *Sere* is essentially identical with *series,* but possesses the great advantage of being distinctive and of combining much more readily, as in *cosere, geosere,* etc.

Sere and cosere.—A sere is a unit succession. It comprises the development of a formation from the appearance of the first pioneers through the final or climax stage. Its normal course is from nudation to stabilization. All concrete successions are seres, though they may differ greatly in development and thus make it necessary to recognize various kinds, as is shown later. On the other hand, a unit succession or sere may recur two or more times on the same spot. Classical examples of this are found in moors and dunes, and in forest burns. A series of unit successions results, in which the units or seres are identical or related in development. They consist normally of the same stages and terminate in the same climax, and hence typify the reproductive process in the formation. Such a series of unit successions, *i. e.,* of seres, in the same spot constitutes an organic entity. For this, the term *consere* or *cosere* (*cum,* together, *sere; consero,* bind into a whole) is proposed, in recognition of the developmental bond between the individual seres. Thus, while the sere is the developmental unit, and is purely ontogenetic, the cosere is the sum of such units throughout the whole life-history of the climax formation, and is hence phylogenetic in some degree. Coseres are likewise related in a developmental series, and thus may form larger groups, eoseres, etc., as indicated in the later discussion (plate 1, A, B).

Processes in succession.—The development of a climax formation consists of several essential processes or functions. Every sere must be initiated, and its life-forms and species selected. It must progress from one stage to another, and finally must terminate in the highest stage possible under the climatic conditions present. Thus, succession is readily analyzed into initiation, selection, continuation, and termination. A complete analysis, however, resolves these into the basic processes of which all but the first are functions of vegetation, namely, (1) nudation, (2) migration, (3) ecesis, (4) competition, (5) reaction, (6) stabilization. These may be successive or interacting. They are successive in initial stages, and they interact in most complex fashion in all later ones. In addition, there are certain cardinal points to be considered in every case. Such are the direction of movement, the stages involved, the vegetation forms or materials, the climax, and the structural units which result.



A. Stages of a sandhill sere as seen in three successive blowouts, Halsey, Nebraska.
B. Section of a peat deposit, serving as a record of the cosere, "Burton Lake," Lancashire, England.

CAUSES OF SUCCESSION.

Relation of causes.—Since succession is a series of complex processes, it follows that there can be no single cause for a particular sere. One cause initiates succession by producing a bare area, another selects the population, a third determines the sequence of stages, and a fourth terminates the development. As already indicated, these four processes—initiating, selecting, continuing, and terminating—are essential to every example of succession. As a consequence, it is difficult to regard any one as paramount. Furthermore, it is hard to determine their relative importance, though their difference in rôle is obvious. It is especially necessary to recognize that the most evident or striking cause may not be the most important. In fact, while the cause or process which produces a bare habitat is the outstanding one to the eye, in any concrete case, it is rather less important if anything than the others. While the two existing classifications of successions (Clements, 1904; Cowles, 1911) have both used the initiating cause as a basis, it seems clear that this is less significant in the life-history of a climax formation than are the others. This matter is discussed in detail in Chapter IX. It will suffice to point out here that the same sere may result from several initial causes.

Kinds of causes.—All of the causative processes of succession may best be distinguished as initiating or initial, continuing or ecesic, and stabilizing or climatic. At first thought, the latter seems not to be a cause at all but an effect. As is shown later, however, the character of a successional development depends more upon the nature of the climatic climax than upon anything else. The latter determines the population from beginning to end, the direction of development, the number and kind of stages, the reactions of the successive stages, etc. Initial causes are those which produce a new or denuded soil upon which invasion is possible. Such are the chief physiographic processes, deposition and erosion, biotic factors such as man and animals, and climatic forces in some degree.

Ecesic causes are those which produce the essential character of vegetational development, namely, the successive waves of invasion leading to a final climax. They have to do with the interaction of population and habitat, and are directive in the highest degree. The primary processes involved are invasion and reaction. The former includes three closely related processes, migration, competition, and ecesis. The last is final and critical, however, and hence is used to designate the causes which continue the development.

Proximate and remote causes.—In dealing with the causes of development, and especially with initial causes, it must be borne in mind that forces in nature are almost inextricably interwoven. In all cases the best scientific method in analysis seems to be to deal with the immediate cause first, and then to trace its origin just as far as it is possible or profitable. Throughout a climax formation, physiography usually produces a large or the larger number of developmental areas. The influence of physiography in this respect is controlled or limited by the climate, which in its turn is determined by major physiographic features such as mountain barriers or ocean currents. These are subordinate as causes to the general terrestrial climates, which are the outcome of the astronomical relations between the sun and the earth. As a consequence, physiography may well be considered the immediate initial cause of

the majority of primary successions, just as the chresard is the controlling cause of vegetation structure, though it is dependent on the one hand upon soil structure, and this upon physiography, and on the other upon the rainfall, etc.

Apart from the gain in clearness of analysis, greater emphasis upon the proximate cause seems warranted by the fact that it is the chresard to which the plant responds, and not the soil-texture or the physiography. In like manner, the invasion of a new area is a direct consequence of the action of the causative process and not of the remote forces behind it. The failure to consider the sequence of causes has produced confusion in the past (*cf.* Chapter III) and will make more confusion in the future as the complex relations of vegetation and habitat come to be studied intensively. The difficulties involved are well illustrated by the following conclusion of Raunkiaer (1909):

"Every formation is before all dependent upon the temperature, and on the humidity originating from the precipitation; the precipitation is distributed in different ways in the soil according to its nature and surface, and hence comes the division into formations. It therefore can not be said that one formation is edaphic and another not; on the other hand, they may all be termed edaphic, dependent as they are on the humidity of the soil; but as the humidity is dependent upon the precipitation, it is most natural to say they are all climatic."

ESSENTIAL NATURE OF SUCCESSION.

Developmental aspect.—The essential nature of succession is indicated by its name. It is a series of invasions, a sequence of plant communities marked by the change from lower to higher life-forms. The essence of succession lies in the interaction of three factors, namely, habitat, life-forms, and species, in the progressive development of a formation. In this development, habitat and population act and react upon each other, alternating as cause and effect until a state of equilbrium is reached. The factors of the habitat are the causes of the responses or functions of the community, and these are the causes of growth and development, and hence of structure, essentially as in the individual. Succession must then be regarded as the development or life-history of the climax formation. It is the basic organic process of vegetation, which results in the adult or final form of this complex organism. All the stages which precede the climax are stages of growth. They have the same essential relation to the final stable structure of the organism that seedling and growing plant have to the adult individual. Moreover, just as the adult plant repeats its development, *i. e.*, reproduces itself, whenever conditions permit, so also does the climax formation. The parallel may be extended much further. The flowering plant may repeat itself completely, may undergo primary reproduction from an initial embryonic cell, or the reproduction may be secondary or partial from a shoot. In like fashion, a climax formation may repeat every one of its essential stages of growth in a primary area, or it may reproduce itself only in its later stages, as in secondary areas. In short, the process of organic development is essentially alike for the individual and the community. The correspondence is obvious when the necessary difference in the complexity of the two organisms is recognized.

Functional aspect.—The motive force in succession, *i. e.,* in the development of the formation as an organism, is to be found in the responses or functions of the group of individuals, just as the power of growth in the individual lies in the responses or functions of various organs. In both individual and community the clue to development is function, as the record of development is structure. Thus, succession is preeminently a process the progress of which is expressed in certain initial and intermediate structures or stages, but is finally recorded in the structure of the climax formation. The process is complex and often obscure, and its component functions yield only to persistent investigation and experiment. In consequence, the student of succession must recognize clearly that developmental stages, like the climax, are only a record of what has already happened. Each stage is, temporarily at least, a stable structure, and the actual processes can be revealed only by following the development of one stage into the succeeding one. In short, succession can be studied properly only by tracing the rise and fall of each stage, and not by a floristic picture of the population at the crest of each invasion.

II. GENERAL HISTORICAL SUMMARY.

In order to give students a general idea of the development of the subject, an account of all the earlier papers accessible is given here. After the work of Hult (1885), studies of succession became more frequent. In this recent period, those works have been selected which mark an advance in the principles or methods used in the investigation of development, or which endeavor to organize the field in some degree. The literature of the peat cosere is so vast, however, that only a few of the more comprehensive works can be mentioned here. This applies especially to the literature of Quaternary and earlier plant horizons, much of which has only an indirect bearing upon the problems of succession. This field has also produced a rich harvest of polemic writings, nearly all of which are ignored, with the exception that many of the titles are listed in the bibliography.

EARLY INVESTIGATIONS.

King, 1685.—While there is abundant evidence that succession in moors and in forest burns had been a matter of observation and comment for many centuries, the earliest recorded work that approaches investigation in its nature was that of King (1685:950) on the bogs and loughs of Ireland. The following excerpts indicate the degree to which he understood the nature and origin of bogs:

"Ireland abounds in springs. Grass and weeds grow rapidly at the outburst of these. In winter, these springs swell and loosen all the earth about them; the sward, consisting of the roots of grasses, is thus lifted up by the water. This sward grows thicker and thicker, till at last it forms a quaking bog. . . . I am almost (from some observations) tempted to believe that the seed of this bog moss, when it falls on dry and parched ground begets the heath. . . . It is to be observed that the bottom of bogs is generally a kind of white clay or rather sandy marl, and that bogs are generally higher than the land about them, and highest in the middle. . . . The true origin of bogs is that those hills that have springs and want culture constantly have them: wherever they are, there are great springs.

"I must confess there are quaking bogs caused otherwise. When a stream or spring runs through a flat, if the passage be not tended, it fills with weeds in summer, trees fall across it and dam it up. Then, in winter, the water stagnates farther and farther every year, till the whole flat be covered. Then there grows up a coarse kind of grass peculiar to these bogs; this grass grows in tufts and their roots consolidate together, and yearly grow higher, in so much that I have seen of them to the height of a man. The grass rots in winter and falls on the tufts, and the seed with it, which springs up next year, and so still makes an addition: Sometimes the tops of flags and grass are interwoven on the surface of the water, and this becomes by degrees thicker, till it lies like a cover on the water; then herbs take root in it, and by a plexus of the roots it becomes very strong, so as to bear a man. These may be easily turned into a meadow, as I have seen several times, merely by clearing a trench to let the water run away. Trees are found sound and entire in them, and those birch or alder that are very subject to rot. I have seen some of the

trees half sunk into the bogs and not quite covered. They are generally found at the bottom, not only of the wet, but even of the dry red bogs."

Degner, 1729.—Degner's dissertation upon peat-bogs, especially those of Holland, appears to have been the first comprehensive treatise upon this subject, though he cited Schook's "Tractatum de Turfis" (1658), and Patin's "Traité de Tourbes Combustibles" (1663), as still earlier works. Degner combated the assumption that "moss is formed of decayed wood" by the following arguments:

"1. It is contrary to the common opinion of the inhabitants of Holland.
"2. Trees are not found in every moss.
"3. Trees are often found buried where no moss is formed.
"4. Where trees abound are the fewest mosses. They seem rather to retard than expedite the formation of mosses.
"5. Some mosses are found to be 30 feet deep before we reach the wood; it seems incredible that such immense quantities of that matter could be formed of wood.
"6. If forests are converted into moss, the greatest part of Muscovy, Tartary and America, and other woody uncultivated regions, would, long ere now, have undergone that change, which is not the case."

Degner described the peat-bogs of Holland minutely, and asserted that they are often renewed when dug. He stated that the pits and ditches are filled with aquatic plants, and that these are converted into peat. He found also that when a large pit was dug, and a large sheet of water was left exposed to the winds, the growth of aquatic plants was retarded and the renewal of the moss checked; while in small pits aquatics developed rapidly and the renewal of the moss was correspondingly rapid. He mentioned as well-known facts the filling of a ditch 10 feet wide by 7 feet deep by aquatic plants in 10 to 30 years to such a degree that men and cattle could safely pass over it, and the digging of peat where a navigable lake once existed.

Buffon, 1742.—Buffon seems to have left the first clear record of the successsion of forest dominants, and of the effect of light and shelter on the process:

"If one wishes to succeed in producing a forest, it is necessary to imitate nature, and to plant shrubs and bushes which can break the force of the wind, diminish that of frost, and moderate the inclemency of the seasons. These bushes are the shelter which guards the young trees, and protects them against heat and cold. An area more or less covered with broom or heath is a forest half made; it may be ten years in advance of a prepared area. (234)

"The best shelter in wet soil is poplar or aspen, and in dry soil *Rhus*, for the growth of oak. One need not fear that the sumac, aspen or poplar can injure the oak or birch. After the latter have passed the first few years in the shade and shelter of the others, they quickly stretch up, and suppress all the surrounding plants. (237, 238).

"The oak and beech are the only trees, with the exception of the pine and others of less value, that one can sow successfully in wild land." (245)

Biberg, 1749.—Biberg (1749 :6, 27) described in brief form the origin of a meadow from a swamp, and indicated the general stages of succession. *Sphagnum* spread over the swamp until it filled the latter with an extremely porous stratum. *Scirpus caespitosus* then extended its roots into this, and together with species of *Eriophorum* formed elevated peat areas. These furnished a

firmer foundation for other invading plants until the whole marsh was converted into a meadow, especially if the water fashioned for itself a broader outlet. He also considered crustose lichens to be the first foundation of vegetation. When the land first emerged from the sea, minute crustose lichens began to clothe the most arid rocks. At length they decayed and formed an extremely thin layer of earth on which foliose lichens could live. These in turn decayed and furnished humus for the growth of mosses, *Hypnum, Bryum,* and *Polytrichum,* which finally produced a soil on which herbs and shrubs could grow.

Anderson, 1794.—Anderson's views upon the origin and nature of peat-bogs may be gained from Rennie (1810:60, 83), who regarded many of them as unconfirmed. He considered moss (moor) to be a plant *sui generis,* which continued to increase to an immense magnitude and indefinite age, but that, in its progress, it enveloped trees and every other matter that came in its way. He reached the conclusion that "nothing can be so absurd, nothing so contradictory to reason, and every known fact respecting the decomposition of vegetables, than the whole of the doctrine that has been implicitly adopted respecting the formation of moss, by means of decaying sphagnum or any other plant whatever." In support of this, he advanced the arguments that:

"1. All vegetable substances, when dead, decrease in bulk so much that they occupy not above one hundredth part of the space they did.
"2. Moss produces few vegetables; these tend to decay rapidly.
"3. The vegetable substance which forms moss must therefore have been *one hundred* times more bulky than the moss itself.
"4. Mosses are found 30, even 40 feet deep.
"5. The most abundant crop on the most fertile soil will not cover the earth, when fresh cut, half an inch deep; when rotten, it only covers the earth one hundredth part of this.
"6. Therefore, it would require 9,600 years to form a moss 20 feet deep on the most fertile soil.
"7. Moss produces not *one hundredth* part of the crop of a fertile soil; therefore, it would require upwards of *900,000 years* to produce 20 feet of moss earth on such a soil."

De Luc, 1806.—From the various accounts of his investigations furnished Rennie by letter, De Luc (Rennie, 1810:137, 128, 116, 30) may well be regarded as the keenest and most indefatigable of early students of peat-bogs, prior to Steenstrup at least. He was probably the first to make use of the term *succession,* and certainly the first to use it with full recognition of its developmental significance. His description of the method by which "lakes and pools are converted into meadows and mosses" is so complete and detailed that frequent quotation can alone do justice to it:

"A *third* kind of peat ground has attracted my attention in the survey I took of Brendeburg, Brunswic, and Shleswig: It is connected with lakes. The bottom of every dale is a meadow on a subsoil of peat; this, by gradually advancing into, contracts the original extent of the lakes; and, it is well-known in that country, that many large lakes have been converted into smaller ones, by the peat advancing from the original shores, and many places now meadows, and only traversed by a stream, had still a lake in them, in the memory of old people.

"I have said that the peat gradually extends forward in these lakes, contracting their surface. This is occasioned by the following causes. The sandy sediment carried into these lakes by streams gradually raises the bottom of them. The consequence of this shallowness is the growth of common reeds; these are like the van in the progress; these advance forward as the bottom of the lake is raised. No peat appears among the reeds, nor even among the small aquatic plants which form a zone behind them.

"2. Behind the zone of reeds, another rises up. It is distinct from the former and it is composed of different aquatic plants, as follows: *Scirpus maritimus, S. caespitosus, S. pauciflorus, Equisetum palustre, E. fluviatile, Eriophorum polystachyon,* and *E. vaginatum;* the last of which retains its form and appearance longest in the remote peat.

"3. Behind this zone, the conferva begins to embrace those plants with its green clouds; this forms the bed in which the different species of aquatic sphagnum grow; these thicken the matting, and favor the growth of common moss plants, on the compact surface.

"4. Behind this, another zone appears; it consists of the same kind of plants; but these are so interwoven that the surface is more compact and bears more weight, though very elastic. On this zone some grasses appear.

"5. Proceeding backward from this zone, the surface becomes more and more compact; many kinds of land plants begin to grow over it, especially when that surface, by being raised, is dry in summer. There the *Ledum palustre, Vaccinium oxycoccon, Comarum palustre, Erica tetralix,* and various kinds of grasses grow. Thus begins a zone on which cattle may pasture in the summer.

"6. From the beginning of this useful zone, still backward the ground becomes more and more solid. This is the last zone that can be distinguished by a decided difference in progress.

"I have said before, that the succession of these different zones, from the border of water towards the original border of sand, represents the succession of changes that have taken place through time in each of the anterior zones, so that, in proportion as the reeds advance, new zones are forming behind the advancing reeds, on the same places which they thus abandon. That process is more rapid in lakes which are originally shallower, and slower in deeper lakes. It seems even to be stopped in some parts, where the reeds, which can not advance beyond a certain depth, approach the brow of a great declivity under water; there the progress, if continued, is not perceptible: But in lakes originally not very deep, and in which the sandy sediments are advancing all around, the reeds, forming a ring, gradually contracting its circumference, meet in the center; and at last these reeds themselves vanish, so that instead of a lake, a meadow occupies its surface. In some of these meadows, attempts have been made to keep up a piece of water, but the attempt is vain, excepting at a great expense: for luxuriant aquatic plants soon occupy that space, and the peat, advancing rapidly, restores the meadow."

De Luc also noted the significance of wet and dry periods in the development of the bog:

"The surface of these pits is covered with all kinds of ligneous and aquatic plants that delight in such a soil; these alternately overtop each other; the ligneous plants make the greatest progress in a *dry summer,* so that the surface seems to be entirely covered with them. The reverse is the case in a rainy summer. The aquatic plants overtop the ligneous and choke them insomuch that the whole surface seems to be entirely covered with a matting of aquatics which, by decaying, form a soil for the ensuing season. If it

continues rainy for a succession of years, these aquatic plants continue to prevail till a dry season comes. This is so certain, that in the succession of beds, or strata of the moss, these different species of plants are distinguishable. These strata are either composed of the roots and fibres of ligneous plants, or of the remains of aquatic; so that upon examining some of the cuts of the deepest canals, one saw *distinctly* the produce of the several years, and could even distinguish the different produce of a wet and dry season, from the residuum each had left."

Rennie, 1810.—Rennie, in his "Essays on the Natural History and Origin of Peat Moss," gave the first comprehensive and detailed account of peat-bogs. His book is an almost inexhaustible mine of opinions and observations from the widest range of sources. It must be read in detail by everyone who wishes to be familiar with the beginnings in this most important part of the field of succession. The titles of the nine essays are as follows:

I. Of Ligneous Plants.
II. Of Aquatic Plants.
III. On the Changes and Combinations by which Vegetable Matter is converted into Moss.
IV. On the Simple and Compound Substances that may be Expected and are Really Found in Peat Moss.
V. On the Alliance Between Peat, Surtur-brandt, Coal, and Jet.
VI. On the Alliance between Peat and Other Bituminous Substances.
VII. On the Distinguishing Qualities of Peat Moss.
VIII. On the Sterility of Moss in its Natural State, and Causes of it.
IX. On the Different Kinds and Classification of Peat Moss.

Rennie discussed at length the relation of forest to peat-bogs, and stated that in many bogs one tier of roots appears perpendicularly above another, while in some even three tiers appear in succession. Trees are also found growing upon the ruins of others after they have been converted into moss. He cited the observations of the Earl of Cromarty with reference to the replacement of forest by bog:

"That, in the year 1651, when he was yet young, he visited the parish of Lochbroom in West Ross; that he there saw a small plain covered with a standing wood of fir trees, which were then so old that they had dropped both leaves and bark. On a visit to this forest 15 years afterwards, not a tree was to be seen, and the whole plain was covered with green moss. By the year 1699, the whole had been converted into a peat moss from which the inhabitants dug peat."

The author quoted many opinions upon the secondary development of peat when the original deposit had been dug, and concluded that the conditions requisite for regeneration were that the pits be full of water, and that the water be stagnant. The process went on most rapidly in small pits with shallow water. A résumé of opinions upon the rate of peat formation was also given, and extensive extracts from De Luc, Poiret, Degner, Anderson, Walker, and others were commented upon. As to the vegetation of mosses, he concluded that many peat-bogs, when dug, are renovated by aquatic plants; that the same species of plants have contributed and still contribute to the original formation of many mosses; that many lakes in the north of Europe have been converted into moss and then into meadows by the growth of these or similar aquatic plants; that aquatic plants may be traced in most, if not all, moss; and that many fertile plains, in the course of ages, have undergone changes

from arable lands to forests, from forests to lakes, from lakes to mosses, from mosses to meadows, and from meadows to their original state of arable land. He likewise supposed that many low levels, covered with wood, had been converted into morasses. In citing examples of such changes, he also made use of the term "succession," in the following sentence: (227)

"The first is Low Modena, which seems to have undergone all these changes; the second is the bog of Monela in Ireland, which seems to have been subjected to a similar succession. Carr, in his 'Stranger in Ireland' (1806:190) says: 'Stumps of trees are still visible on the surface of the bog of Monela; under these lies a stratum of turf 10 or 15 feet deep; under this a tier of prostrate trees is discovered; beneath these another stratum of earth is found of considerable depth; and below this a great number of stumps of trees are found, standing erect as they grew. Thus, there is a succession of three distinct forests lying in ruins, one above the other.' (229) There are other circumstances which render it equally probable that one generation has risen upon the ruins of another. In many mosses one tier of roots appears perpendicularly above another; yet both are fixed in the subsoil. In some even three tiers appear, in succession, the one above another." (27)

Dureau, 1825.—Dureau de la Malle (1825:353), attracted by the work of Young on the effect of rotation upon crops, endeavored to trace the same principle in woodland and meadow. As a landed proprietor in Perche, he possessed unusual advantages for this purpose, both in the utilization of the forests and in experiments designed to prove that the alternative succession of plants is due to the long retention by seeds of the power of germination. In cutting the woods of Perche, composed of *Quercus, Fagus, Castanea, Ulmus,* and *Fraxinus,* only oaks and beeches were left as seed trees. The cut-over areas came to be occupied by *Genista, Digitalis, Senecio, Vaccinium,* and *Erica,* and finally by *Betula* and *Populus tremula.* At the end of 30 years, the birch and aspen were cut, and quickly succeeded themselves. The oak and beech returned only after the third cut, 60 years later, and became masters of the area. Since there were no adjacent aspens and birches, the author believed their seeds could not have been brought by the wind, and he concluded that the seeds remained dormant in the soil for at least a century. He noted also the reappearance of rushes, sedges, and grasses in clear areas in the heath, and stated that he had observed the grasses and legumes of a natural meadow successively lose and gain the preeminence for five or six times in 30 years. The results of his observations and experiments are summed up as follows:

"The germinative faculty of the seeds of many species in a large number of families can be retained for 20 years under water, or for at least a hundred years in the soil, provided they are not subject to the action of atmospheric factors.

"The alternance or alternative succession in the reproduction of plants, especially when one forces them to live in societies, is a general law of nature, a condition essential to their conservation and development. This law applies equally to trees, shrubs, and undershrubs, controls the vegetation of social plants, of artificial and natural prairies, of annual, biennial, or perennial species living socially or even isolated. This theory, the basis of all good agriculture, and reduced to a fact by the proved success of the rotation of crops, is a fundamental law imposed upon vegetation."

Steenstrup, 1842.—Steenstrup (1842:19) was the first student of peat-bogs to turn his attention to the succession of fossil horizons preserved in the peat. His pioneer work is the classic in this much-cultivated field, and since it is practically inaccessible, a fairly full abstract of it is given here. The memoir consists of five parts, viz., (1) Introduction; (2) Description of Vidnesdam Moor; (3) Description of Lillemose Moor; (4) Comparative development of Vidnesdam and Lillemose Moors; (5) General observations upon the Tree-, Scrub-, and Heath-moors of Denmark. It is chiefly the detailed descriptions and comparison of the moors which are summarized in the following pages:

The bottom of Vidnesdam consists of a layer of bluish clay, containing leaves of a grass and of *Myriophyllum* and fruits of *Chara*. Above this lies a layer of fresh-water lime, inclosing a very large number of leaves of *Potamogeton obtusifolius zosterifolius,* and perhaps of *Sparganium natans.*

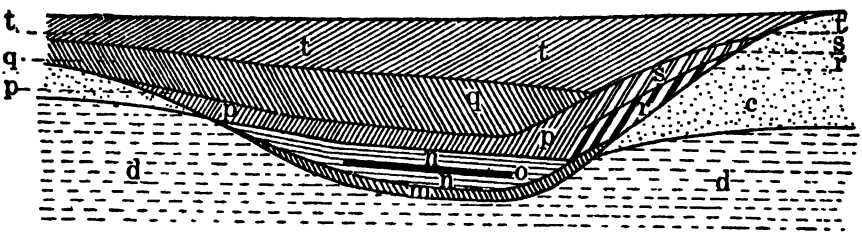


FIG. 1.—Section of Vidnesdam moor, showing various layers of the cosere. After Steenstrup.

The leaves and stems are incrusted with lime, and are stratified in this layer, in which *Chara* and *Myriophyllum* also occur. An interruption in the formation of the lime layer is indicated by a lamina of *Hypnum fluitans* and *Myriophyllum verticillatum.* In the cross-section of the bottom of the moor (fig. 1), these three layers are designated by *m*, *n*, and *o* respectively. The best series of layers, however, is the marginal one, which follows the slopes all around the moor. The drift *c* is covered by a layer of cones, needles, and branches of conifers, 1 to 1.5 feet in depth. In this are embedded large coniferous roots, the trunks of which lie in the spongy peat layers toward the center. The large number of trunks found upon a small area leads to the conclusion that the pine (*Pinus silvestris*) grew in a dense, pure stand. The pine trunks found in this layer *r* extend into a layer of peat which lies directly above the lime layer *n*. The lower part of the peat layer is filled with grass-like leaves, but the upper part consists wholly of *Sphagnum.* Above, the latter is mixed with *Hypnum cordifolium,* which finally becomes predominant and forms the layer *q*. The position of the *Sphagnum* below and about the pine trunks indicates that this layer must have been forming before as well as at the time of burial of the trees, while the *Hypnum* layer must have developed subsequently. Pine roots also occur in this layer, but the pines to which these stumps belonged must have grown at a later period and under much less favorable conditions than those of the forests preserved in layer *r*.

An oak period must have followed that in which these stunted pines grew, as oak trunks occur directly above layer *q*. Oak leaves and fruits were rare about the trunks, but on the marginal slopes remains of the oak (*Quercus sessiliflora*) dominate the layer *s*. They become recognizable only with difficulty in the upper part of the layer, which then passes gradually into an alder layer *t*. The latter is the top layer of the moor, covering the oak one to a

depth of 3 to 4 feet, both at the margin and in the center. Oaks occur occasionally in this layer, though the alders are wholly predominant, their branches, leaves, and catkins sometimes forming the peat alone. The large number of nuts indicates that hazel (*Corylus avellana*) probably formed a considerable portion of this layer, especially near the margins. In the northern portion of the moor the *Hypnum* layer contained leaves of *Eriophorum angustifolium*, and scattered trunks of *Betula*.

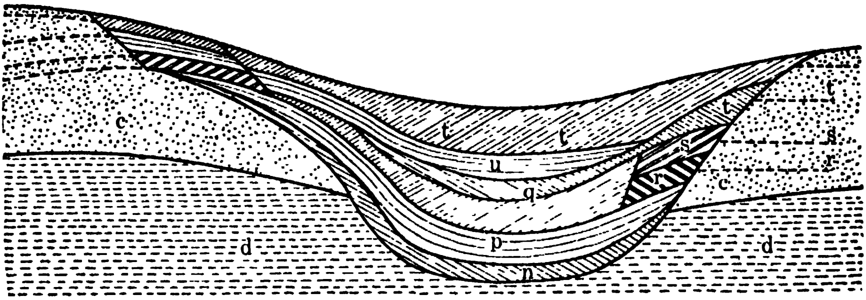


FIG. 2.—Section of Lillemose moor, showing central and marginal layers of the cosere. After Steenstrup.

In the Lillemose Moor, the structure is indicated by the cross-section shown in figure 2, in which the following layers are seen, from below upward:

Central Area.	Margins.
t'. *Sphagnum* with alder	*t*. Alder.
u. *Hypnum proliferum* with remains of birch and oak.	
q. *Sphagnum* with oak, above with *Oxycoccus*, *Eriophorum*, etc	*s*. Oak.
p. *Hypnum cordifolium* with pine and some aspen	*r*. Pine.
n. Silica layer with *Potamogeton* and aspen	*c*. Drift.
d. Sandy clay, the substratum	*d*. Sandy clay.

The lower part of layer *n* seems almost a continuation of *d*, but the upper portion clearly shows the remains of *Hypnum cordifolium*, *Potamogeton*, *Equisetum*, *Myriophyllum*, *Alisma*, and especially leaves and twigs of *Populus tremula* everywhere in the layer, showing that the latter grew upon the marginal slopes. This foliated silica layer is covered by a peat layer of *Hypnum*, *p*, which is also in direct contact with the substratum over some parts of the banks. Pine needles and cones occur with the *Hypnum*, and on the margin become so abundant as to form a layer *r*, which consists almost wholly of pine cones, needles, and bark, mixed with some *Hypnum fluitans*. The pine layer also contains remains of *Betula*, *Salix*, and *Menyanthes*. Above the pine stratum lies the oak layer, containing twigs, leaves, acorns, cups, and an occasional trunk of *Quercus sessiliflora*. The next layer is that of alder peat, composed almost wholly of *Alnus glutinosa*, but with an occasional *Betula* or *Salix*. This uppermost layer covers the entire surface of the moor as well as the margins. In the center of the moor, the layer *n* is covered by *Hypnum* peat, *p*, which is pure below, except for roots of *Nymphaea*, leaves of *Populus* and *Salix*, and fruits of *Betula*. In the upper part occur pine leaves and trunks. The next layer, *q*, is composed of *Sphagnum*, with *Oxycoccus vulgaris*, *Andromeda polifolia*, *Scirpus caespitosus*, and *Eriophorum angustifolium* in the upper portion, together with some oak and birch. This is followed by a layer *u* of *Hypnum proliferum*, with remains of both oak and birch, and this is in turn covered by an extensive layer of alder peat *t'*.

The peat layers of the two moors not only afford a record of the successive populations which occupied the basin, but also of the different forests which clothed its margins. In the basin proper, Vidnesdam shows but two strata of moss peat, namely, the *Sphagnum* and the *Hypnum cordifolium* layers, while in Lillemose there are three strata and in the reverse order, viz., *Hypnum cordifolium*, *Sphagnum*, and *Hypnum proliferum*. As to the margins, it is assumed that the banks were without vegetation during the period in which no plants had appeared in the water of the basin. With the early stages of water vegetation, forest seems to have appeared on the banks, for the quantity of aspen leaves found in layer *n* shows that this tree must have been dominant. These give way about the middle of layer *p* to abundant pine needles, indicating that the aspens had been replaced by pine, as would be expected in the normal succession. The marginal layer *r* testifies to the length of the period for which the pine dominated the margin, but it finally yielded to the oak, as is shown by the plant remains in layer *q*. The marginal layer *s* is perhaps due wholly to the oak forest, but this seems to have been destroyed by increasing moisture, resulting in a *Hypnum* layer, which was finally succeeded by *Sphagnum* and alders.

There is thus no doubt that these two moors have developed during a period in which several forest vegetations have arisen and disappeared. The aspen forests may be regarded as preparatory to the pine and oak forests, which probably dominated the region for thousands of years, but have practically disappeared from the country to-day. While these forests, as well as the moor vegetations, belong in a definite time sequence, it is practically impossible to assign any absolute time for any or all of the layers.

The four forest vegetations, viz., aspen, pine, oak, and alder, found above each other in Vidnesdam and Lillemose, occur in all the forest moors of north Sjelland, and other evidence points to their former occurrence throughout Denmark. These four forests not only succeeded each other in the moors, but everything points to a synchronous succession on the uplands, so that one may speak of a pine period, for example, for the whole country. The final alder forest of the moor was succeeded by the beech forest which is now the dominant one. However, no trace of the beech has been found in the moors. Thus there seems no doubt that one vegetation succeeded another in such a way that the later grew on the ruins of the former, and that the replacement of one by the other was the result of a slow natural cycle. In this cycle one organization develops and then gradually calls forth conditions which cause its disappearance and hasten the development of a new organization.

Reissek 1856.—Reissek (1856:622) studied in detail the formation and succession of islands in the Danube. These arose through separation from the mainland, or through the deposition of gravel and sand. It was thought that islands due to deposition were laid down irregularly and without sorting, and that their formation bore no direct relation to the development of vegetation. The author found the process of formation both definite and regular, and the influence of the vegetation fundamental. Each island was at first a sand-bar due to high water or ice action. The first vegetation consisted of scattered willows, most frequently *Salix purpurea*. The willows became bushy and caught the water-borne sand, building hummocks which gradually united to form a sandy level 6 to 8 feet above the gravel. The willows themselves came to be half-buried in the sand. All other invaders established themselves in the sand among the willow crowns. They entered in a definite succession, so that a sequence of stages results, each with its characteristic

woody plants. *Salix purpurea, S. riparia,* and *Myrica germanica* belonged solely to the first stage. The second stage consisted of *Alnus incana, Populus alba,* and *Cornus sanguinea,* and the last stage of *Fraxinus excelsior, Ulmus campestris, Acer campestre, Quercus pedunculata, Pirus malus, P. communis,* etc. High water and drift-ice often destroyed young islands entirely or partly, exposing the gravel-bank on which the sere might be repeated. Partial destruction of the sandy plain permitted the development to begin again in new areas alongside of those in later stages. The pioneer willows died off as soon as the trees of the second stage developed much shade, a fate which also overtook the groups of *Phragmites* which occurred among the willows.

Vaupell, 1857.—In discussing the invasion of the beech into Denmark, Vaupell (1857:55) reviewed the evidence obtained from submerged forests, deposits of calcareous tufa, and peat-bogs. The ancient forests of Denmark, and especially of Jutland, were a mixture of coniferous and deciduous species. *Betula* was the most common, with *Quercus* and *Pinus silvestris* next in importance; the aspen, willow, hazel, elm, and maple played but a secondary part. In existing forests *Fagus* is the universal dominant. Since remains of the beech are lacking in peat, tufa, and in the submerged forests, Vaupell concluded that it had entered Denmark at a subsequent time. In seeking an explanation of the change of dominance, he cited the opinions of Dureau de la Malle, Laurent, and Cotta in favor of the natural "alternation of essences," but reached the conclusion that it must be produced by other causes than the exhaustion of the soil. Where the beech invades forests of birch, it gains the upper hand by overshadowing the birch trees, suppressing them and causing their death. The birch fails also to reproduce because its seedlings do not thrive in the dense shade of the beech. The plantations of pine are likewise invaded by the beech with similar results, unless protected by man. In the cases where beech has yielded to pine, the explanation is always to be found in intervention by man. The author concluded that the beech had migrated from its center in France and Germany during the present geological period, establishing itself wherever the soil became drier or richer, and dispossessing the birches and pines everywhere but in marshy or sterile soil.

von Post, 1861.—von Post (1861) appears to have been the first to give a complete and detailed account of the reactions by which plants and animals produce soils. Ramann (1888) has summarized his work upon the coprogenous formation of the various biogenous soils. Muck (Schlamm, gyttja) consists of plant fragments, including diatom shells. It forms very elastic masses which are deposited on the bottom in waters, springs, brooks, lakes, etc. Muck is formed by the deposition of insect excreta, together with the remains of dead infusoria, crustacea, and insects, diatom shells, and algæ. Such muck deposits are often found beneath peat moors; "Lebertorf" is a kind of fossil muck. Moor soil is deposited more rapidly than muck in waters colored brown by humus material. Moor soil consists of a dark-brown, soft mass which dries into a hard mass with extreme shrinkage, which is then no longer plastic in water. It consists of finely divided plant remains arising from the excrement of water animals, particles of humus material, and, for the remainder, of the same materials as muck. The animal excrement, however, is more abundant, the diatoms less. Moor soil is formed chiefly in lakes and ponds in forests, when they contain much humus material in solution

which is precipitated by lime salts. Peat consists of brown organic masses of plant remains which have not been eaten. It is deposited in a mass consisting predominantly of animal excrement, and contains diatoms and animal remains in small degree. Peat arises in waters which are more or less clothed with aquatic plants. Besides the common grass-peat, the moss-peat of the coniferous forests is characteristic for Sweden. In ponds containing *Calla* and *Menyanthes* there develops a vegetation of *Sphagnum*, upon which later *Calluna* and *Ledum*, as well as spruces and pines, establish themselves. In more northern regions, lichens overgrow the moss-peat, especially *Cladonia rangiferina* and *Biatora icmadophila*. A peculiar kind of peat is carr-peat, which consists of the roots of sedges, *Calamagrostis arctica, Deschampsia flexuosa,* etc. Mull or humus consists of digested plant-parts and animal remains, together with brown granular amorphous particles, which are to be regarded as precipitates of humus salts. These are insoluble in water, acid, and alkali. Between these constituents occurs an equal amount of animal excrement. The various kinds of humus are moss and lichen humus which consist predominantly of animal remains, coniferous forest humus consisting of decomposed wood, mycelia, etc. Deciduous forest humus, darker than the foregoing, is rich in excrement and animal remains, and contains much humic acid. Grass-humus consists chiefly of animal excrement mixed with sand and clay.

Gremblich, 1876.—Gremblich (1876, 1878:1014) called attention to the succession in a particular area of different formations, each of which prepared the way for the following one:

"We see certain formations invade an area, dominate it for a while, and then disappear, until finally the rotation of formations falls into inactivity, in order perhaps to begin a new cycle which takes the same course. If one follows the course of succession in a moor, he will notice that in general three clearly marked phases may be distinguished. The first phase has for its task the preparation of the bare ground for vegetation. The second is marked by a cover which shows great luxuriance, both of species and individuals. In the last phase appears a plant covering which closes the rotation of organic life, and marks the death of the succession. The last two stages as a rule store up carbon dioxid in some form, *e. g.*, wood, peat or humus. Each succession in a particular area shows close relationship with that of the moor, and the development of the latter may be taken as the type for all successions. We venture to say that moor succession or some parallel development takes place wherever man leaves nature to her own course."

Gremblich also described the invasion of talus in the Dolomites of the Tyrol, and pointed out the three successive phases of development. The first phase was marked by lichens and low herbs, *Thlaspi, Galium, Saxifraga,* etc. The humus thus produced was invaded by *Adenostyles, Ranunculus, Saxifraga, Rhododendron, Rosa, Rhamnus, Crataegus, Alnus,* and *Pinus,* as the most important species of the second phase. The last phase was marked by the entrance of *Sphagnum,* or of *Nardus, Scirpus caespitosus, Azalea procumbens, Empetrum nigrum,* etc., which form peat, often a meter deep. The last plants, *Azalea* and *Empetrum,* finally disappear and the naked peat alone remains, to be again colonized when soil is drifted upon it by the wind.

Müller, 1878-1887.—Müller (1878, 1884, 1887) made a critical investigation of the humus soils of beech and oak woods and of heath, which is of the first importance for the study of the factors which affect invasion and replace-

ment in forests. The soil of the beech forest is distinguished as of two types. In the first, the surface is covered with a layer of leaves and twigs which build an incoherent mass. This covers the upper soil, which consists of loose earth, and is 3 to 5 feet or more deep. Sometimes the entire upper soil is dark gray-brown, but frequently only the uppermost layer has this color. The latter is then called mull. It has a characteristic ground-cover of *Asperula, Mercurialis, Milium, Melica, Stellaria, Anemone,* etc. It is defined by Müller as follows: "Beech mull is a loose incoherent layer of converted leaves, twigs, etc., of the beech forest, rich in animal life and with the organic material intimately mixed with the mineral earth." In the second type, the leaf litter is lacking. The soil is firm, filmy, and absorbs rain like a sponge. The upper part is composed of a tenacious brown-black layer of humus. The vegetation consists characteristically of *Aira, Trientalis, Maianthemum, Potentilla,* etc., and many mosses. The beech thrives poorly in contrast with its growth in beech mull, and the old trees are mostly in a pathological condition. Beech turf is regarded as consisting of a leaf-mold of the beech woods which is poor in animal life; it is united into a firm peat by roots and by a very persistent mycelium. It is significant that the reproduction of beech upon mull is easy, while upon peat young trees can not come to maturity. This indicates that the peat was formerly clothed with mull. If a beech forest upon mull is completely cut off so that no beech peat is naturally formed, there appears another vegetation which in its turn prepares the soil and opens the way for other forms. The mull may retain its essential character or may be converted into heath peat. After the destruction of beech forest upon beech peat, no new forest can appear, as a rule, but the soil is densely clothed with *Aira flexuosa,* and the peat layer is finally destroyed by the grass. In similar thorough fashion, the author considered the soil of oak woods and of heath in reference to the changes in them which affect the succession.

Other investigations.—From 1802 to 1885, when Hult's classic work upon the developmental study of vegetation was published, there appeared a large number of works in which succession was treated more or less incidentally. These dealt mostly with peat-bogs, or with succession after fire or disturbance by man. Among the former were the important monographs or handbooks of Eiselen (1802), Dau (1823), Wiegmann (1837), Lesquereux (1844), Grisebach (1845), Vaupell (1851), Lorenz (1853, 1858), Pokorny (1858, 1860), and Senft (1861, 1862). The others may be mentioned briefly here. De Candolle (1820:27) mentioned the cultures on the dunes of the "Landes," in which the rapidly growing *Genista,* after having served as cover for seedlings of *Pinus,* was finally driven out by the latter. Lund (1835) and Reinhardt (1856) studied the origin of the Brazilian *campos* or savannahs, the former concluding that they had been derived from forest as a consequence of fire, while the latter regarded the effect of fire as secondary. Berg (1844) studied the successive modifications of the deciduous forests of the Harz in connection with their disappearance before the conifers. He showed that the forests remained unchanged just as long as they were undisturbed by man, and that, while trees with winged migrules readily invaded wind-throw areas, they were gradually replaced by the species of the surrounding forest. Humboldt (1850:10) dealt with succession only incidentally, though he clearly recognized it as universal:

"In northern regions, the absence of plants is compensated for by the covering of *Bæomyces roseus, Cenomyce rangiferinus, Lecidea muscorum, L. icmadophila* and other cryptogamia, which are spread over the earth and may be said to prepare the way for the growth of grasses and other herbaceous plants. In the tropical world, some few oily plants supply the place of the lowly lichen." (125) "Thus one organic tissue rises, like strata, over the other, and as the human race in its development must pass through definite stages of civilization, so also is the gradual distribution of plants dependent upon definite physical laws. In spots where lofty forest trees now rear their towering summits, the sole covering of the barren rock was once the tender lichen; the long and immeasurable interval was filled up by the growth of grasses, herbaceous plants, and shrubs."

Henfrey (1852:56) considered briefly the changes in vegetation due to man:

"It is certain that the appropriate stations of many plants would be destroyed with the removal of forests, and new conditions of soil created for the habitation of immigrants from other regions. But the modification of the surface so as to alter the physical condition of the soil is by far the most important change brought about in reclaiming land for cultivation. The banking out of the sea changes by degrees the vegetation of its shores; bare sand-dunes, where scarcely a plant could maintain a precarious footing, are by degrees covered with vegetation; sandy inland wastes are rescued from the heath and furze, and made to contribute at first by coniferous woods, such as the larch, and when the soil has become by degrees enriched, by the plants requiring a better nourishment, to the general stock of wealth; and in these changes many species are destroyed, while others naturally making their way into a fitting station, or brought designedly by the hand of man, grow up and displace the original inhabitants."

De Candolle (1855:472) cited the conclusions of Dureau de la Malle (1825), Laurent (1849), and Meugy (1850) as to the "alternation of forest essences," a subject much discussed in the works on forestry of this time. He failed, however, to recognize the fundamental nature of succession, for he regarded the alternation (succession) of forest dominants as a process distinct from that which occurs when a forest is burned or cut. It seems probable that the difference he had in mind is that which distinguishes primary from secondary succession. Hoffmann (1856:189) found *Rubus* to be the first invader in forest burns in the Ural Mountains; this was followed successively by *Amelanchier, Alnus, Betula,* and other deciduous trees, and these were finally replaced by pines and other conifers. Hill (1858) first pointed out that the second growth in forest burns or cuttings is normally composed of genera different from those found in the original vegetation. Stossner (1859) described in detail the conversion of a fallow field covered with *Viola* into a mountain meadow.

Middendorff (1864:641) considered the succession of dominants to be the exception rather than the rule in the case of burn forests in Siberia, and explained the cases in which other species replaced the original forest dominants as due to the influence of man. Kabsch (1865:75) pointed out the primary rôle of lichens in succession on rock surfaces:

"Lichens are the real pioneers in vegetation; they corrode the hardest basalt as they do the softest limestone, decompose the rock, and mix its particles with their own remains, in such a way as to give opportunity for the growth of a higher vegetation."

Engler's pioneer work (1879) upon the developmental history of vegetation deals primarily with the geological development and the relationship of floras, but has little bearing upon succession. Nathorst (1870, 1873) was the first to demonstrate the presence of arctic plants, *Salix herbacea*, *S. polaris*, *S. reticulata*, and *Dryas octopetala*, in beds of postglacial clay in southern Sweden. These and other arctic species were also found at the bottom of moors in Seeland. Nathorst discovered *Betula nana*, *Salix retusa*, *S. reticulata*, *Polygonum viviparum*, and *Loiseleuria procumbens* in layers resting directly upon glacial deposits in Switzerland. *Salix polaris* was also found under the glacial boulder clay at Cromer in England, and various other willows between the clay and the "forest beds."

RECENT INVESTIGATIONS.

Blytt, 1876.—Blytt (1876, 1881) advanced the theory that since the glacial period the climate of Norway has undergone secular changes in such fashion that dry periods of continental climate have alternated with moist periods of insular or oceanic climate, and that this has happened not once but repeatedly. As long as land connections permitted a mass invasion, continental species entered during one period and insular species during the other. This theory is supported by investigations of the peat-beds of Norway, the oldest of which have an average depth of 16 feet. They consist of four layers of peat with three intervening layers of remains of rootstocks and forests. The surface of the drier moors is more or less completely covered with heather, lichens, and forest. With increasing moisture, forest and heath disappeared, and were replaced by moor, while at the same time species of *Sphagnum* dominated the wetter places almost wholly. The root layers, on the other hand, represent periods when the moor was drier than formerly, and during which peat formation probably ceased for thousands of years, to begin again later. In the oldest moors there are traces of three such dry periods, and such moors are often covered to-day with forests for the fourth time.

The explanation of such changes has been sought in local causes, but Blytt is convinced that it lies in the alternation of dry and wet periods. When the rainfall and humidity changed, the surface of the moor must have become drier or wetter in consequence, and have produced the vegetation found in the alternating layers of peat and forest remains. The absence of forest beds in the wet moors, and their presence only in the dry ones, seem to indicate that this has not been produced by local causes. The moors of Norway are at present drier than formerly, and are mostly covered with forest or heath, while the *Sphagnum* layer just below the surface indicates that the period just preceding was a wetter one. In the second place, Norway has been elevated since the glacial period, and the greater depth of peat-beds at high altitudes is taken as an indication that the formation of peat began long before the land reached its present level.

The four layers of peat investigated by Steenstrup in Denmark are separated by forest layers which agree with those of Norway. The profile for the two countries is as follows:

1. The present. The moors are mostly dry and contain a new root layer ready to be buried under peat deposits as soon as the new moist period begins.

2. Peat. Probable period of the invasion of sub-Atlantic flora, apparently prehistoric, because stone implements are found in the young layers.
3. Stumps with forest remains.
4. Peat with trunks and leaves of *Quercus sessiliflora.*
5. Stumps with forest remains, hazel, oak, etc.
6. Peat with pine trunks.
7. Stumps and forest remains.
8. Peat with leaves of *Populus tremula* and *Betula odorata.*
9. Clay with arctic plants, *Dryas octopetala, Salix reticulata, Betula nana,* etc.
10. Closing stages of the glacial period; moist climate.

Blytt's theory has been the storm center of the study of Scandinavian and Danish moors. It has been accepted and modified by Sernander (1891, 1894, 1895, 1899, etc.), and vigorously combated by Andersson (1893, 1896, 1898, 1903, etc.). Blytt (1892) found further support for his view in an investigation of the calcareous tufas of Norway. Johanson (1888), Hulth (1899), Holmboe (1904), Lewis (1905-1911), Haglund (1909), Samuelsson (1911), and others have studied boreal moors with especial reference to the theory of alternating wet and dry periods.

Hult, 1885-1887.—To Hult belongs the great credit of being the first to fully recognize the fundamental importance of development in vegetation, and to make a systematic study of a region upon this basis. He maintained that the distribution of plant communities could be understood only by tracing the development from the first sparse colonies upon bare soil or in water to the now dominant formations. He also laid down some of the general principles upon which the developmental study of vegetation must be based, and was the first to grasp the significance of the climax. In his classic investigation of the vegetation of Blekinge in Finland (1885:161), Hult traced the succession of each intermediate formation through its various stages to the supposed climax. He found that grassland on poor soil became heath; on rich soil, oak wood. The heath developed into forest, dominated by *Betula* alone, or mixed with *Picea, Pinus,* or *Quercus. Betula* is displaced upon dry sandy soil by *Pinus,* upon moist soil by *Picea.* The spruce forest reacts upon the soil in such a way as to favor the invasion of *Fagus,* which eventually replaces the spruce. The birch forest can also be replaced by oak forest, which gradually develops into beechwood. Where the oak becomes dominant in grassland or heath, it develops into a scrub, which appears to yield finally to beech scrub. On dry banks, the scrub is replaced by birch, this by spruce, and the latter finally gives way before the beech. The *Menyanthes* community of wet banks is followed by *Carex,* and this by meadow moor, which yields to birch forest. The latter in turn is replaced by spruce forest, which seems to persist as the climax. The sequence of development in the moor is (1) aquatic formation, (2) *Carex* moor, (3) hummock moor, (4) peat moor, (5) pine moor, (6) birch forest, (7) spruce forest. In the swamps, the succession is as follows: (1) *Potamogeton,* (2) *Sphagnum-Amblystegium,* (3) *Menyanthes-Eriophorum,* (4) *Carex-Sphagnum,* (5) peat moor, (6) birch forest, (7) spruce forest.

The following were regarded as climax communities, but it seems obvious that the beech forest is the only real climatic climax: (1) rock heath, (2) pine forest on dry sand or on peat moor, (3) spruce forest on shallow shore moors,

(4) birch forest on deep moors, (5) woodland along streams, (6) thorn scrub in warm, dry places, (7) beech forest in all other places. The behavior of the beech as the climax dominant is the same in Finland that Steenstrup and Vaupell have shown for Denmark and Fries for Sweden. Hult thought that this does not indicate a change of climate, but merely the return of the beech into areas from which it was largely removed by lumbering.

Hult (1887:153) also traced the development of the alpine vegetation of northernmost Finland. He found that in the drier places *Cladineta* and *Alectorieta* finally replaced all other communities, while in moist areas grass and herb consocies passed into communities of dwarf shrubs, or even into a lichen climax. The development everywhere was marked by a transition from more hygrophilous to more xerophilous conditions. The initial stage of succession was determined by the local conditions of colonization. The sequence itself was regarded as everywhere constant; in no place did a backward development take place.

Warming, 1891.—Warming (1891, 1895, 1907) was the first to give a consistent account of succession on sand-dunes, and his pioneer studies in this field have served as a model for the investigation of dune seres in all parts of the world. He found that the shifting or white dunes began as heaps of sand formed by tides, waves, and wind; the particles as a rule are less than one-third of a millimeter in diameter. The further growth of such dunes is made possible by sand binders, such as *Psamma arenaria, Elymus arenarius, Carex arenaria, Agropyrum junceum, Lathyrus maritimus, Alsine peploides,* etc. The last two are found only on the lower dunes, and are sooner or later driven out by *Psamma* and *Elymus*, which are especially adapted to the building of high dunes, because of their ability to push up through a cover of sand. *Psamma,* however, is the most important pioneer, and excels all others in its ability to collect sand among its tufted leaves, and to grow up through it. Other plants find their way in among the shoots of *Psamma* and *Elymus,* and, as the sand becomes more and more fixed, conquer the intervening spaces. The more effectively these two grasses fix the soil, the more they prepare it for other species, which ultimately replace them. Lichens, mosses, and perennials which form tufts or mats, or possess a multicipital primary root, establish themselves at this stage, and the dune passes into a stable or gray dune.

Warming recognized two principal associations (consocies) among those of the shifting dune, viz, *Psammetum* and *Elymetum.* Woody species such as *Hippophaë rhamnoides, Salix repens,* and *Empetrum nigrum* appear here and there, and give rise to scrub. The gray dune may pass into dune-heath or dune-scrub, and then into dune-forest. In the north of Europe may be encountered the following formations, which show a zonal succession to some extent. It is obvious that the zonal order is essentially that of the developmental sequence.

1. Sand algæ.
2. Iron-sulphur bacteria.
3. Psammophilous halophytes.
4. Shifting or white sand-dunes.
5. Stationary or gray dunes.
6. Dune-heath and dry sand-field.
7. Dune-scrub.
8. Dune-forest.

MacMillan, 1894-1896.—MacMillan's studies of the bogs and muskeags of Minnesota constitute the pioneer work upon succession in America, though

analysis at this early period was necessarily general. In the investigation of *Sphagnum* atolls (1894:2), he concluded that these atolls, *i. e.,* circular zones of *Sphagnum,* are due to a season of gradual recession of the waters of the pond, followed by a season of comparatively rapid increase in area and level. This is indicated by the fact that the vegetation of the atoll differs from that of the pond outside and the lagoon within it. The atoll first appeared as a zone of floating bog, which was separated from the shoreward turf as a consequence of the original zonation of the shore plants and of the rise of the water-level, taken in conjunction with certain special topographic conditions. The sequence of events was probably as follows: The pond, as a result of silting-up and of climatic variations, slowly diminished until its shore-line coincided with the inner edge of the present atoll. The size of the pond at this time is indicated by the existing lagoon. The shore vegetation then invaded the bare slopes and formed characteristic zones, the inner perhaps of *Sphagnum.* When the pond began to fill up again, the marginal zone of turf was forced upward, and finally detached to form a circular floating bog or atoll. The further rise in level left the atoll well out in the pond. The atoll sank as its weight increased with its growth in thickness, and it finally became anchored to the bottom of the pond. While it is possible that the two atolls were formed simultaneously, one is now in the stage characterized by *Sarracenia, Eriophorum,* and *Kalmia,* and the other is dominated by *Ledum* and *Picea.*

MacMillan (1896:500) also studied the *Sphagnum* moors or muskeags of Minnesota, in which almost every stage may be found from open lakes with continuous sandy beaches to solid masses of spruce and tamarack. The latter is displaced by pines or hardwood, and is finally developed into mixed wood or perhaps into meadow. Typical muskeag with spruce and tamarack are regarded as an intermediate type between the original open lake and the later forest. The center of the muskeag is usually softer than the edges, though in many, even of the small ones, the center is quite firmly filled with soil, and *Sphagnum* predominates here. When a central pool is present, it contains *Utricularia* and *Lemna,* and often *Potamogeton* and *Nymphaea.* The next zone contains *Kalmia* and *Andromeda,* with *Carex, Eriophorum, Sarracenia, Salix, Vaccinium,* etc. *Ledum* is found on drier peripheral portions, and is often the most abundant heath when the *Sphagnum* has disappeared. This zone is surrounded by spruces, usually *Picea mariana,* sometimes *P. canadensis,* tamarack, *Larix laricina, Alnus incana, Betula,* and *Salix.* An examination of *Sphagnum* moors shows that they are characterized by zones of *Larix, Picea, Ledum, Andromeda,* and *Utricularia,* from the margin to the center. The tamarack and spruce zones are slowly closing in upon the others, and will eventually occupy the whole area, as is evidenced by the circular or elliptical tamarack communities frequent in southern Minnesota. After the tamarack area has become solid, the *Sphagnum* often persists in little clumps and mats at the bases of the trees. *Sarracenia, Vaccinium,* etc., also linger for some time, but *Eriophorum, Salix,* and many other species disappear because of the shade.

As to the origin of a solid or spruce-centered consocies of tamarack, it is doubtful whether a stage with central moor ever existed. In some cases, successions of muskeag openings with intervening tamarack arise from the filling of a lake with bars or reefs upon its bottom. Some of the circular tamarack

swamps with or without spruce cores were not necessarily derived from moors with tamarack or tamarack-spruce border-rings, though most of the solid tamarack swamps must have developed by the closing in of a ring of timber upon a constantly diminishing moor. Finally, the author remarks significantly that "the contemplation of vegetation in any region with these principles in view is certainly interesting. Practically it connects at once ecologic distribution with physiography, and enlarges the content both of topography and botany."

Warming, 1895.—Warming made the first attempt (*cf.* 1896:350; 1909: 348) to deal with succession in a general fashion, though his treatment was brief and largely incidental to the main purpose of his work. This is emphasized by the fact that the text devoted to this subject is practically unchanged in the second edition of his book, in spite of a lapse of 14 years marked by a great advance in developmental ecology. Nevertheless, Warming deserves great credit for being the first to try to organize this vast field. In the last edition the section which deals with development is headed "Struggle between plant-communities," and is subdivided into 7 chapters, namely: (1) Conditions of the Struggle; (2) The Peopling of New Soil; (3) Changes in Vegetation Induced by Slow Changes in Soil Fully Occupied by Plants, or Succession of Vegetation; (4) Change of Vegetation without Change of Climate or Soil; (5) The Weapons of Species; (6) Rare Species; (7) Origin of Species. The last two obviously have only a remote connection with succession as a process. The discussion of the peopling of new soil deals with the origin of bare soil areas and the vegetation which arises upon them. The following chapter upon the succession of vegetation treats primarily of water and rock seres, and especially of the conversion of moor and forest. The chapter on the peopling of new soil is divided into (1) vegetation on sand, (2) production of marsh, (3) lowering of water-level, (4) volcanic eruptions, (5) landslips, (6) fires in forest and grassland, (7) other sources of new soil, (8) summary of results. In the latter, six fundamental principles are laid down; these deal with the pioneers, number of species, life-forms, migration-forms, light relations, and the distinction into initial, transitional, and final communities. The copious citation of papers on development makes the treatment a very helpful introduction to the subject.

Graebner, 1895.—Graebner (1895:58) was the first to make a comprehensive study of the development of a great climax or subclimax community. The developmental relations of the heath of northern Germany are considered in three sections: (1) Origin of the Heath Formation; (2) Changes of Heath Vegetation; (3) Culture of Heath; while the physical factors are discussed under (1) Soils of the Heath; (2) Dependence of Heath upon Climatic Conditions; (3) Requirements of Heath Plants. The origin of the heath is dealt with under the following heads: (1) Origin of Heath from Forest; (2) Origin of Heath on Bare Sand; (3) Origin of Heath-moor or Moss-moor: (*a*) in water, (*b*) on bare soil, (*c*) from forest; (4) Origin of Heath from Heath-moor. The details of many of these developmental processes are quoted in Chapter VIII. The utilization of the heath is discussed under (1) afforestation, (2) cutting of sods, (3) burning, and (4) meadow.

Pound and Clements, 1898-1900.—Pound and Clements (1898:216; 1900: 315) also attempted to deal with the origin of formations in a general manner.

They distinguished formations as either *primitive* or *recent,* with respect to origin. By the former was understood the origin in the geological past, while recent origin has to do with development at the present time. Formations were said to arise at the present time either by *nascence* or by *modification.* Origin by nascence occurs only upon bare areas, while origin by modification occurs through changes in existing communities. Formations regularly disappear through the agency of fires, floods, man, etc., and in all such cases new formations arise by nascence. Two sets of factors are concerned in the origin of formations by modification, viz, natural and artificial. Natural factors are either biological or physical; artificial factors are due to the presence or agency of man or animals. Biotic forces may transform facies or patches into formations, or they may change the latter by bringing about the intrusion of other facies. Patches (colonies) are invariably incipient formations, and in many situations have become actual formations.

The physical forces are either meteorologic or physiographic. A rapid change from one extreme to another affords the best example of the influence of climatic forces. While the instances cited illustrate in a slight degree the bearing of climatology upon formations, it is impossible to estimate fully and accurately the influence of climatic changes operating through a long period or of a sudden reversal of such conditions. Modification of formations by physiographic forces is illustrated in the canyons of the Niobrara, where the sandy soil has become covered with a layer of loam. Modification due to artificial factors is of several sorts. It may arise through the direct agency of man, as in the case of culture formations, or through his presence, as in most waste formations. The prairie-dog-town waste is an example of a formation produced by animal agency. The origin and development of the vegetation in blow-outs and sand-draws were described in detail (1898:258; 1900:365). The same authors (1898^2:19) devised the quadrat method for the quantitative study of plant communities, and of ecotones especially, and applied it as the basic method for determining the structure and development of vegetation.

Schimper, 1898.—Schimper (1898) has distinguished two ecological groups of formations, viz, "climatic or district formations, the character of whose vegetation is governed by atmospheric precipitations, and edaphic or local formations, whose vegetation is chiefly determined by the nature of the soil." Climatic formations belong to one of three types, forest, grassland, and desert. A good forest climate is regarded as consisting of a warm growing-season, a continuously moist subsoil, and damp, calm air, especially in winter. A climate with dry winters is hostile because trees can not replace the moisture lost by transpiration. A good grassland climate consists of frequent, even though slight, precipitations during the growing-season, so that the superficial soil is kept moist, and a moderate degree of heat as well. Drouth during spring or early summer is unfavorable to grassland. A woodland climate leads to victory for woodland, a grassland climate to victory for grassland. In transition climates, edaphic influences decide the outcome. Strong deviations from woodland or grassland climate produce desert. Definite properties of the soil may bring forth a character of vegetation that belongs to none of the climatic types. These demand a soil congenial to the vast majority of plants. Extreme soil conditions unfavorable to most plants set vegetation free from the controlling influence of rainfall. Consequently, the vegetation of rocks,

gravel, swamps, etc., bears in the highest degree the impress of the substratum, and this impress usually remains identical under very different climatic humidities, which on such soils play only a subordinate part.

In spite of the successional significance of climatic and edaphic communities, Schimper (*l. c.*, 185) seems to have had only a general idea of the development of vegetation, for he not only states that little attention had been paid to it, but also cites only Treub's study of Krakatoa and the work of Flahault and Combres on the Camargue as examples of it. While his open edaphic formations are in the main stages in successional development, as he recognizes in certain cases, fringing forests are portions of climax and hence climatic formations, as is well shown by every large stream of the prairie region. The fact that he does not regard edaphic formations as mostly or primarily developmental is shown by the subdivision into edaphic formations due to telluric water (swamps, moors) and open edaphic formations (rocks, dunes). The latter alone are regarded as showing a transition from edaphic to climatic formations. How close he came to the basic distinction between developmental and climax communities, and how his concept of edaphic and climatic formations caused him to miss the real relation may be gathered from the following excerpt:

"Transition from Edaphic to Climatic Formations: Between the bare hard rock and the finely grained soil that finally results from it, for the possession of which there is a struggle between woodland and grassland, according to what has been said above, there is a series of open transitional formations, which possess the character neither of woodland nor of grassland, and which assume nearly the same appearance even in dissimilar climates, and owe their individuality chiefly to the mechanical texture of the soil. The transformation of these transitional formations into the definite ones of woodland and grassland is continually proceeding under our eyes, but so slowly that we can observe only a part of the process directly, and can form an estimate of their sequence only by comparing their condition at different ages. In spite of the highly interesting nature of the development of formations, very slight attention has hitherto been paid to it."

Schimper's climatic formations are for the most part the climax formations of the present treatise, and his edaphic and transition formations are developmental units, associes, and consocies. This is essentially the conclusion reached by Skottsberg, though in different terms (1910:5).

Cowles, 1899.—The first comprehensive study of succession in America was that of Cowles (1899:95) upon the sand-dunes of Lake Michigan. Together with the dune studies of Warming already mentioned, it has served as a model for the investigation of dune succession the world over. The methods of physiography were employed, inasmuch as the flora of a particular area was regarded "not as a changeless landscape feature, but rather as a panorama, never twice alike." The author concluded that " the ecologist must study the order of succession of the plant societies in the development of a region, and that he must endeavor to discover the laws which govern the panoramic changes. Ecology is, therefore, a study in dynamics." The ecological factors of the dunes were considered under the heads: (1) light and heat, (2) wind, (3) soil, (4) water, (5) other factors. The plant societies and their developmental relations were treated in full under the following captions:

A. The beach.
  1. The lower beach.
  2. The middle beach.
  3. The upper beach.
  4. Fossil beaches.
B. The embryonic or stationary beach dunes.
  1. Dunes of rapid growth (primary embryonic dunes).
  2. Dunes of slow growth (secondary embryonic dunes).
C. The active or wandering dunes; the dune complex.
  1. Transformation of stationary into wandering dunes.
  2. Physical and biological features of the dune complex.
  3. Encroachment on preexisting plant societies.
  4. Capture of the dune complex by vegetation.
D. The established dunes.
  1. The basswood-maple series.
  2. The evergreen series.
  3. The oak dunes.

Cowles, 1901.—Cowles's work (1901:73) upon the physiographic ecology of Chicago and vicinity stands out as a landmark in the developmental study of vegetation. It forced the recognition of physiography as the most striking cause of vegetation changes, and the use of the term "physiographic ecology" constantly challenged the attention of students to the attractiveness and significance of successional studies. Cowles deserves great credit at the hands of ecologists for his early and consistent championing of the cause of development in vegetation. Even though physiography can not yield a complete picture of succession, as Cowles himself recognized (1901:81; 1911:168), its processes are so striking and interesting, and its action as an initial cause of development so universal and decisive, that it must always receive a large share of attention from students of succession. The author's conclusions as to progression and regression are considered in detail in Chapter VIII. As a consequence, the following outline will suffice to afford a general idea of the work, and to indicate its basic nature.

I. The content and scope of physiographic ecology.
II. The plant societies.
  A. The inland group.
    1. The river series.
      (1) The ravine.
      (2) The river-bluff.
      (3) The flood-plain.
    2. The pond-swamp-prairie series.
      (1) The pond.
      (2) The undrained swamp.
      (3) The prairie.

II. The plant societies—*Continued.*
    3. The upland series.
      (1) The rock hill.
      (2) The clay hill.
      (3) The sand hill.
  B. The coastal group.
    1. The lake-bluff series.
    2. The beach-dune-sandhill series.
      (1) The beach.
      (2) The embryonic or stationary beach areas.
      (3) The active or wandering dunes; the dune complex.
Summary and conclusion.

Clements, 1902-1904.—In "Herbaria Formationum Coloradensium" (1902) and its continuation, "Cryptogamae Formationum Coloradensium" (1906-1908), Clements endeavored to organize an herbarium method of indicating and recording the structure and development of vegetation. This method was discussed briefly in "Formation and Succession Herbaria" (1904), and the analysis of the Colorado vegetation proposed in the collections mentioned was sketched in its main details. The formations recognized were largely climax associations of the mountain clisere, and were arranged in the corresponding sequence. Many of them, however, were the developmental associations, now distinguished as associes, and these were grouped in the seral

sequence. The structure of each was indicated by the grouping of the species into facies, aspects, principal and secondary species, marking consocies, socies, clans, and colonies respectively.

Clements, 1904.—In the "Development and Structure of Vegetation," Clements made the first attempt to organize the whole field of present-day succession, and to connect the structure of vegetation with its development in the essential way that these are related in the individual plant. The concept was advanced that vegetation is an entity, whose changes and structures are in accord with certain basic principles in much the same fashion that the functions and structures of plants follow definite laws. The treatment falls into five divisions, association, invasion, succession, zonation, and alternation. Of these, invasion and succession are developmental processes, and association, zonation, and alternation the basic expressions of structure which result from them. Invasion was defined as the movement of plants from one area to another, and their colonization in the latter. Invasion was analyzed into migration, or actual movement into a new place, and ecesis, the establishment in the new home. Migration was considered with reference to mobility, organs modified for dissemination, migration device, agents, and direction. Barriers, endemism, and polygenesis were discussed in connection with ecesis, while invasion was further considered with reference to kinds and manner. The necessity of using quadrats and migration circles for the exact study of invasion was also emphasized.

After a historical summary of the development of the idea of succession, the latter was related to invasion, and successions were classified as normal, divided into primary and secondary, and anomalous. Primary and secondary successions were grouped upon the basis of agent or process, *e. g.*, elevation, volcanic action, weathering (residuary soils), gravity (colluvial soils), water (alluvial soils), etc. (*cf.* Chapter IX). The reactions of seral stages were next analyzed in detail, and the laws of succession were grouped under the following heads: (1) causation, (2) reaction, (3) proximity and mobility, (4) ecesis, (5) stabilization, (6) general laws. The treatment was concluded by a discussion of classification and nomenclature and of methods of investigation.

Früh and Schröter, 1904.—Although they did not deal specifically with succession, the monumental monograph of Früh and Schröter upon the Swiss moors is a mine of successional material of the first importance. It will suffice here to indicate the scope and nature of the work by giving its main heads.

First part: General treatment.
1. Definitions.
2. Peat-producing plant formations of Switzerland.
   (1) Moor and Peat Communities of the Midland, and Jura.
      a. Low moor.
         (*a*) Deposition and forlanding communities.
         (*b*) Low moor communities.
      b. High moor.
   (2) Moor and peat formation in the alpine region.
3. Peat.

First part: General treatment—*Continued.*
4. Stratigraphy.
5. Geographical distribution of the Swiss moors.
6. Sketch of a geomorphologic classification of all moors.
7. Relation of colonists to moors in the light of their toponymy.
8. Utilization of Swiss moors.
9. Postglacial vegetation strata of northern Switzerland, and significance of moors in their reconstruction.

Second part: Description of certain Swiss moors.

Clements, 1905-1907.—The treatment in "Development and Structure of Vegetation" was adopted in "Research Methods in Ecology," but a further attempt was made to place the study of vegetation upon a completely developmental and quantitative basis. The formation was regarded as a complex organism, possessing functions and structures, and passing through a cycle of development similar to that of the plant. The formation as a result was definitely based upon the habitat as the cause, and a detailed analysis of it was made from the standpoint of functions, viz, association, invasion (migration and ecesis) and succession (reaction and competition), and of structures, zonation and alternation. The formation was analyzed into minor units, society, community, and family, for the first time, and the classification and nomenclature of units were considered in detail.

Especial emphasis was placed upon instrumental and quadrat methods of exact investigation, in which the constant interaction of habitat, plant, and community must furnish the primary basis. Instrumental methods of habitat measurement were organized and developed, and the quadrat method of analyzing and recording the structure and development of vegetation was advanced to the place of first importance in the investigation of succession (161). Quadrats were differentiated as list, chart, permanent, denuded, and aquatic quadrats of various size, and were modified into line, belt, permanent, denuded, and layer transects of varying width and length. A further endeavor was made to increase the accuracy and finality of developmental studies by organizing an experimental attack upon them, as in "Experimental Evolution" (145) and "Experimental Vegetation" (306), by means of methods of natural, artificial, and control habitats. Essentially, the same ground was covered in "Plant Physiology and Ecology" (1907), though the vegetational material was condensed and rearranged, as shown by the following outline:

X. Methods of studying vegetation.
XI. The plant formation.
XII. Aggregation and migration.
XIII. Competition and ecesis.
XIV. Invasion and succession.
XV. Alternation and zonation.

Moss, 1907-1910.—Moss is entitled to much credit for being the first to clearly include the idea of development in the concept of the formation and to distinguish formations upon this basis. The importance of his contribution in this respect was obscured by an inclusive conception of the habitat, which resulted in his restricting the development of the formation to a few final stages. However, the germ of the complete developmental view is to be found in his distinction of chief and subordinate associations. His views are much discussed in Chapters VII and VIII. Hence it will suffice here to point out that his concept of the formation was first advanced in 1907 (12), developed in 1910, and applied to the vegetation of the Peak district in 1913.

Clements, 1910.—In the "Life History of Lodgepole Burn Forests," Clements endeavored to lay down a set of principles and to furnish a model for the exact study of succession by means of instruments and quadrats. Apart from the use of the latter, especial emphasis was placed upon the method of reconstructing the history of a burned area by means of the annual rings of woody plants and perennials, and by means of fire-scars and soil-layers. Seed production, distribution, and germination were regarded as the critical points of attack, and the consumption of seeds and fruits by rodents and birds

was held to be of paramount importance. Reaction and competition were studied quantitatively for the first time in successional investigation, and these were related to the rate of growth and of development.

Cowles, 1911.—In "The Causes of Vegetative Cycles," Cowles performed a distinct service in drawing attention clearly to the three great causes of succession, namely, climate, physiography, and biota. While the importance of these had been recognized (Pound and Clements, 1898:218; 1900:317; Clements, 1904:124), they had not been used for the primary groups in classification, nor had their developmental relations been emphasized. While it is repeatedly stated in the following chapters that the causal grouping of seres is less fundamental and satisfactory than a developmental one, there can be no question of its attractiveness and convenience. In fact, it is a necessary though not the chief part of a consistently developmental classification. Cowles's ideas are discussed at some length in Chapters VII, VII, and IX, and hence only the main topics of his treatment are indicated here.

1. Demonstration of vegetative cycles.
2. Development of dynamic plant geography.
3. Delimitation of successional factors.
4. Regional successions.
5. Topographic successions.
6. Biotic successions.
7. Conclusion.

Shantz, 1911.—In his paper upon "Natural Vegetation as an Indicator," Shantz gave the results of the first quantitative study of the reactions and successions of a great grassland vegetation. In addition, his studies furnished convincing proof of the basic importance of instrumental and quadrat methods in investigation, and yielded practical results in a new field of the first consequence. The study of water penetration, of the relation of root systems to it, and of the influence of developing vegetation upon it was a brilliant analysis of reaction, and will long serve as a model for all investigators. The graphic representation of these relations in a double transect, or "bisect," constitutes a new method of record of great value.

Tansley, 1911.—Tansley and his colleagues, in "Types of British Vegetation," were the first to apply the developmental concept to the treatment of a great vegetation. Moss's concept of the formation was used in organizing the material, and this, combined with a thorough understanding of the basic importance of succession, gave to the treatment a distinctively developmental character. In this respect, the book is practically unrivaled among accounts of extensive vegetations, and its value must always remain great, even if the concept of the formation is revised in the light of increased knowledge. Much of the work also appeals to the exact ecologist because of the use of instrumental and quadrat methods. Tansley's views upon the units of vegetation are discussed in Chapter VII.

MacDougal, 1914.—The work of MacDougal and his associates upon the Salton Sea is outstanding in several respects. It is unique in dealing with xerotropic succession from a wet saline habitat to a climax of desert scrub. Still more remarkable has been the opportunity offered by the flooding of the Salton Basin and the gradual recession of the lake year by year, thus affording a complete record of the stages of development in the series of zones from the newest strand of 1913 to the oldest of 1907. It is even more significant, however, that the monograph is the result of the cooperation of ten specialists

in the various fields represented in this complex problem. This foreshadows the future practice of ecology, when the study of vegetation has become so largely quantitative that the investigation of the habitat in its climatic, edaphic, and physiographic relations must be turned over to the experts in these fields. The comprehensive nature of the research is indicated by the following outline: geologic history, geographical features, sketch of the geology and soils, chemical composition of the water, variations in composition and concentration of water, behavior of micro-organisms, action of Salton Sea water on vegetable tissues, tufa deposits, plant ecology and floristics, movements of vegetation due to submersion and desiccation of land areas.

III. INITIAL CAUSES.

Significance of bare areas.—Seres originate only in bare areas or in those in which the original population is destroyed. They may be continued, with or without change of direction, by less critical modification of the habitat or by the invasion of alien species. It is a universal law that all bare places give rise to new communities, except those which present the most extreme conditions of water, temperature, light, or soil. Of such there are few. Even fields of ice and snow show algal pioneers, rocks in the driest desert bear lichens, caves contain fungi, and all but the saltiest soils permit the entrance of halophytes. From the standpoint of succession, water is the most important of bare habitats, and it is almost never too extreme for plant life, as is shown by the invasion of the hot springs of Yellowstone Park by various algæ.

Habitats are (1) originally bare or (2) bare by denudation. The former are illustrated by water, land produced by rapid emergence, such as islands, continental borders, etc., lava flows and intrusions, deltas, ground moraines, etc., dunes, loess, etc. Denuded habitats arise in the most various ways, and are best exemplified by bad lands, flooded areas, burns, fallow fields, wastes, etc. The essential difference between the two is that the new area is not alone developmentally different in never having borne a plant community, but is also physically different in lacking the reactions due to successive plant populations. The last consideration is of profound importance in the development of the new vegetation, and serves as a primary basis for distinguishing successions (plate 2, A, B).

Modifications of development.—While a new sere can arise only after the destruction of a community in whole or in part, striking changes in the course or rate of succession may occur in existing communities. These are only modifications of development, and are not to be mistaken for the beginnings of new successions. A successional stage may persist beyond the usual period, and become a temporary climax, or, more rarely, it may become the actual climax. On the other hand, the rate of development may be accelerated, and certain normal stages may be combined or omitted. New stages are sometimes interpolated, or the usual climax may be succeeded by a new climax. The direction of development may itself be changed anywhere in its course, and may then terminate in the usual climax, or rarely in a new one. These are all changes within the succession, and are continuative. They must be kept distinct from the destructive changes, which free the habitat for new invasions and can alone initiate succession. Developmental modifications are produced either by changes in the habitat factors or by changes in the usual course of invasion. It is possible also that the two may act together. The habitat may be modified in the direction of the successional reaction and correspondingly hasten the rate of development, or contrary to the reaction and thus reduce the rate, fix an earlier climax, or change the direction. In the case of invasion it is obvious that the failure of the dominants of a particular stage to reach the area would produce striking disturbances in development. Likewise, the appearance of alien dominants or potential climax species would profoundly affect the usual life-history.

Processes as causes.—In the strictest sense there is perhaps but a single universal initial cause of succession, namely, a bare area in which pioneers can establish themselves. It is somewhat confusing, if not illogical, to term a passive area a cause, and in consequence the term is referred back to the active processes and agents which produce the bare area. The latter is the initial fact in so far as the development is concerned, but its cause leaves a directive result in the form of the physical factors which characterize the new area. It must also be recognized that succession does not necessarily occur in every bare area. Two other prerequisites must also be met: there must be an adjacent or accessible plant population and the physical conditions of the habitat must permit ecesis. These are almost universal concomitants of bare habitats, the rare exceptions occurring only in the salt-incrusted beds of old lakes in arid regions and perhaps in ice-bound polar areas. Further exceptions are naturally furnished by wave or tide swept shores and rocks, but these are hardly to be regarded as bare areas.

Change of conditions.—In a denuded area, moreover, succession proper can not occur unless the physical conditions are essentially changed. This is especially true when the adjacent population is mobile. In such cases a short apparent succession may result, owing to differences in rate of germination and growth, but in some cases, at least, the migrants all enter the same year. Thus in certain lodgepole pine burns of the Rocky Mountains, firegrass, fireweed, aspen, and lodgepole pine appear together the first year after the fire, but there is an apparent sere of three or four stages, due merely to differences in rate of growth and consequent dominance. A wholly different example is found in certain deserts with one or two distinct rainy seasons, characterized by annuals. This is typical of the deserts of Arizona and adjacent parts of Mexico and California, in which communities of summer and winter annuals appear each season, only to disappear before the subsequent drought. These represent the pioneer stage of a succession which can not develop further because of extreme conditions.

A bare area, then, must not merely permit the invasion of an adjacent population; it must also present conditions that are essentially different if succession is to result. This is typically the case, since the conditions of formation of new soil differentiate it from the habitats of neighboring communities, while the removal of the plant covering materially modifies the habitat, with rare exceptions. As a consequence, an initiating process must accomplish two results: it must produce a bare area capable of ecesis, and it must furnish it with physical factors essentially different, in quantity at least, from the adjacent areas. In short, a bare area, whether new or denuded, to be capable of succession must be more extreme than the surrounding habitats. This departure from the mean is best seen in the denuding of climax formations, in which case the climatic control is disturbed. In the grass formation of central Nebraska, denudation by wind erosion produces a departure toward the xerophytic extreme, and by flooding, one toward the hydrophytic extreme.

Fundamental nature of water-content.—In the vast majority of bare areas the departure has to do with water-content, usually its quantity but often its quality, as in saline and acid areas. Light is less frequently concerned, while changes of other efficient factors—temperature, nutrients, and aëration—appear to be subordinate. In all cases the production of a more extreme con-

A. Primary bare area, due to weathering, Mount Garfield, Pike's Peak, Colorado.
B. Secondary bare area, due to wind erosion, Morainal Valley, Pike's Peak, Colorado.

dition in the new area has two consequences of the first importance. It determines the conditions of ecesis and hence the life-forms and species which can act as pioneers. It likewise determines the direction of development from drier to wetter or wetter to drier, and consequently the reactions possible. The degree of departure from the climatic mean controls the life-history and determines the number of stages possible between the pioneer and the climax vegetation.

The most critical factor in origin, then, is the amount of water-content in comparison with the mean for the climax area. This is directly affected by the texture of the soil, and this by the initial process or agent. The two extremes possible are water at one end and rock at the other. The former has an excess of water-content and a lack of solid material for fixing the habitat; the latter has a surplus of stability and a deficit of water. Between the two occur all possible combinations of water and solid materials in the form of the various soils. While there is no ecological warrant for excluding rock and water from soils, it will perhaps be clearer if the term is restricted to the usual meaning of a mixture of comminuted rock and water. Apart from the amount of water present in a new area, the stability of the substratum itself must be taken into account. This is of the first consequence in extremely mobile soils, such as those of dunes and blow-outs, where it determines the form and sequence of the pioneers and calls forth a peculiar reaction. The usual course of successional development is a response to the increase or decrease of the holard, *i. e.*, to the ratio between water and rock, as already suggested. This ratio expresses itself in three chief forms, water, rock, and soil. These produce primary distinctions in the development of vegetation, and are used as the physical basis of the system proposed in Chapter IX.

Kinds of initial causes.—All initiating processes and agents agree in their fundamental relation to succession, viz, the production of a bare area characterized by a more extreme condition, usually as to the holard. Moreover, processes very different in themselves produce areas essentially similar or identical as to the sere developed. A pond or lakelet may be formed by physiographic processes, such as flooding, filling, or erosion, by a swing of climate, by a rise in the water-table, by the action of ice, of gravity as in talus, by beavers, or by man in a variety of ways. Many of these do, and all of them may, occur in the same climax area, and would then result in identical or similar seres. A sandy bank may be formed by currents, waves, ice, wind, gravity, or biotic agencies, but the agent has relatively little effect upon the succession. It is the wet, loose condition of the bare sand and the surrounding vegetation which determine the development. The secondary importance of the process is further indicated by the behavior of dune-sand when carried by the wind into streams or lakes or heaped into dunes. The water-content of the two areas is so controlling that the resulting seres converge only at or near the climax. In case base-leveling is regarded as a process, it is obvious that here is a process that produces the most diverse bare areas and seres.

The classification of initial causes from the standpoint of the development of vegetation necessarily groups together the most diverse agents and processes. This is shown to be the case in the classification of seres outlined later. For the sake of a complete account of initial causes it is most convenient to treat them here from the standpoint of the nature of the agent or process,

however necessary it may prove to combine them later because of their effect successionally. In consequence, such causes may be distinguished as (1) physiographic, (2) climatic, (3) edaphic, (4) biotic. In the analysis of each an attempt is made to distinguish between processes and agents in so far as possible. Special attention is given to the results of each in terms of kind of bare area and the degree of departure from the holard or other mean. This is followed by a discussion of the directive effect upon succession in connection with an endeavor to point out the essential nature of each process from the standpoint of vegetational development. While every effort has been made to appreciate the viewpoints of the physiographer and the climatologist, it is felt that these are necessarily subordinate to the main object of analyzing the development of vegetation.

Physiography.—It is necessary at the outset to indicate the scope assigned to physiography in the present treatise, since the several definitions of the term differ greatly. Physiography is here understood much in the sense used by Salisbury (1907:4), who defines it as having "to do primarily with the surface of the lithosphere, and the relations of air and water to it. Its field is the zone of contact of air and water with land, and of air with water." In this definition the emphasis is considered to be upon the phrase "zone of contact," and climate is not regarded as covered by the definition. While physiography and climate are in constant and universal interrelation, they are regarded as coordinate fields. An initial cause is termed physiographic when it originates a sere in consequence of a changing land form, as in dunes, the cutting down of a lake outlet, or the formation of a delta. It is termed climatic when succession results from denudation due to a climatic change which critically affects the water or temperature relations of a community.

Cowles (1911:168) has evidently felt something of the difficulty inhering in the various uses of the term physiography, for he contrasts topographic with climatic. He apparently also furnishes an example of the double use of physiographic. After speaking of biotic changes and climatic changes as initial causes of succession, he says: "A *third* and *equally diverse* kind of succession phenomena was recorded by Reissek in his study of islands in the Danube, for here there was clearly recognized the influence of physiographic change in vegetation." Here physiographic seems clearly coordinate with climatic and biotic, while in the next two sentences it is used to include climatic: "Thus, in succession we may distinguish the influence of physiographic and biotic agencies. The physiographic agencies have two aspects, namely, regional (chiefly climatic) and topographic." Since physiography and topography are here regarded as essentially synonymous, it seems desirable for the sake of clearness to speak of topographic causes and processes hereafter.

TOPOGRAPHIC CAUSES.

Topographic processes.—All the forces which mold land surfaces have one of two effects. They may add to the land or take away from it. The same topographic agent may do both, as when a stream erodes in its upper course and deposits a delta at its mouth, or undercuts one shore and forms a mud-bank or sand-bank along the other. In similar fashion, a glacier may scoop out a pond or a lake in one region and deposit the material as a moraine

in another. The wind may sweep sand from a shore or blow-out and heap it up elsewhere, or it may carry dust from dry lake-beds or flood-plains for long distances and pile it in great masses of loess. Gravity in conjunction with weathering removes the faces of cliffs and accumulates the coarse material in talus slopes at the base.

Volcanoes and ground-waters in the form of hot springs and mineral springs act similarly to the extent that material is taken from one place and added to another. They differ from the agents cited above, however, in that the removal is from the interior of the earth's crust as a rule, and bare areas are consequently produced only by addition. Perhaps the formation of sink-holes may well be regarded as an exception, where the collapse of the surface results directly or indirectly in denudation. Volcanoes change land forms principally by means of lava-flows and deposits of volcanic dust, and mineral springs by deposition of dissolved material as travertine, sinter, etc. In the case of weathering, the process itself neither adds nor subtracts, but is so intimately and universally associated with transportive agents—water, wind, ice, and gravity—that the effect is the same. Residuary soils furnish the only example of weathering without transport, but these are of little importance in succession.

Kinds of processes.—The various processes which control land forms, and hence the surface available for succession, are (1) erosion, (2) deposit, (3) flooding, (4) drainage, (5) elevation, and (6) subsidence. From the standpoint of physiography, it is evident that these are more or less related in pairs of complementary processes. Erosion in the upper part of a valley has its inevitable effect in the deposition which characterizes the lower part. The formation of a lake by flooding has its normal outcome in drainage by the cutting down of the stream which flows from it, unless filling or evaporation proceed too rapidly. Elevation and subsidence are theoretically complementary at least, and on the Scandinavian coast it is assumed that they are associated at the present time. As will be shown later, elevation and subsidence have practically no effect upon succession at the present, except in the rare cases where new land suddenly appears. Moreover, grave doubt has been thrown upon many of the supposed evidences of coastal changes of level.

While erosion and deposit, flooding and drainage are complementary in the life-history of a river system, as processes they are opposite or antagonistic. The clue to their influence upon vegetation is not to be found in the fact that they are associated in the base-leveling of a region. It resides, on the contrary, in the fact that one is destructive of vegetation or habitat and the other constructive as to habitat. In general, erosion lays bare or destroys an existing habitat, deposition produces a new one. Flooding destroys an existing habitat and drainage lays bare a new one. The fact that all produce bare areas upon which successions can arise is no evidence of their relationship from the standpoint of vegetation. Bare habitats are also produced by climate, fire, man, or animals, without indicating any essential relationship among them. Viewed as topographic processes merely, the sharp contrast between erosion and deposition is obvious. Indeed, in this respect, they are exact opposites. Erosion removes the surface of a land form or decreases its area, or it may do both in the same case. Deposit adds to the surface, or increases the area of the land form, or both. Their union in the development of a river system

has furnished a basic and fertile viewpoint for physiography, but it seems to possess no such value for vegetation.

Base-leveling.—The complex topographic development of a region known as base-leveling seems to present a fundamental explanation of those seres initiated by topographic changes. But the relation between base-leveling and the development of vegetation is apparent rather than real. The connection between them appears to be incidental but not fundamental. There is no such correspondence between the life-history of the Mississippi system and its vegetation as an intrinsic relation between the two would demand. The seral development from origin to climax is a wholly different thing in northern Minnesota from that found in Louisiana, in spite of similarly swampy habitats, and must always remain so while the present climatic relations persist. This seems even truer of mature streams which flow northward, such as the Mackenzie, in which the upper and lower courses must develop in the midst of very different climax formations. In the case of the great drainage basin of the Mississippi, differences in climate and climax vegetation make the course of succession very different in areas of the same age topographically. On the other hand, the valley of the Platte is much more mature than that of the Niobrara or Running Water, but both streams flow through the same climax formations with the same developmental history.

Similar evidence is afforded by lakes and flood-plains developed at different stages in the life-history of a river. According to Davis (1887), a young drainage system contains many lakes which disappear by filling and draining as the river matures. New lakes may then form by the damming back of tributaries, by the cutting off of meanders to form ox-bow lakes, and by the production of lakes in the delta. At any time in the course of the development, lakes may also arise by accidents, such as lava-flows, ice, landslips, work of man, etc. In the same climax region the succession in all these lakes will be essentially identical, regardless of their relation to the life-history of the river. It can be changed only by a decisive change in climate which produces a new climax formation. In the prairie region the succession in cut-off lakes of mature rivers duplicates in all essentials the development in lakes belonging to the youth of tributary streams.

The one striking connection between base-leveling and succession seems to lie in the fact that bare areas for colonization are naturally most abundant when erosion and deposition are most active. Since erosion is typical of hills and deposition of valleys, bare areas produced by erosion tend to be drier than the mean, and those produced by deposition to be wetter. In consequence, just as hill and lowland tend to reach a mean in a temporary base-level, so vegetation tends to a mean, which is usually mesophytic. That it is the extremes and the climatic mean which control, however, and not the topographic process, is shown in semiarid and desert regions. In the Santa Catalina and Santa Rita ranges of Arizona the torrential rains cut back deep canyons and carry out the detritus in enormous alluvial fans known as bajadas. The vegetation of the bajada, instead of being more mesophytic than that of the forested slopes or the moist upper canyons, is intensely xerophytic. A similar condition exists in the Uncompahgre Plateau of Colorado, where the extensive table-land is covered with spruce and fir forest with a rainfall of 30 inches or more, while the streams carry eroded material away into an *Artemisia-Atriplex* vegetation with a rainfall of 12 inches.

If we consider wind erosion and deposit instead of that by water, it seems to afford the clue to the puzzle. While wind erosion is of much less importance, it still plays a large part, as seen in the hundreds of thousands of square miles covered by dunes, sand-hills, and loess deposits. Here the process is totally opposed to base-leveling, as the sand or dust is blown from strand or plains into dunes or hills. The significant fact is that the hills and crests are driest, the hollows wettest. Controlled by water-content extremes, seres of totally different initial stages arise in these two areas, converge more and more as they develop, and terminate in the same climax. In consequence the actual explanation appears to lie in the fact that in the usual erosion by water, soil and water move together. The water which falls on a hill leaves the crest or slope with the soil it has eroded away. When it reaches the ravine, stream, or lowland it deposits its load, only to be itself entrapped in large degree. Thus, it is evident that topography, with soil texture, is the great middleman distributing rainfall to the various habitats as water-content. It is this relation which one finds repeated again and again in a drainage basin, in youth, in maturity, and in old age, wherever erosion and deposition occur. The age of the basin seems to affect the relation only in so far as it determines the number or steepness of slopes on which erosion can occur, or the area of lowland where deposits can accumulate.

EROSION.

Nature.—The removal of soil or rock by the wearing away of the land surface is erosion. In the case of rock it is often preceded by *weathering*, but the process consists essentially of *corrasion*, the picking up of the loose or loosened material and of its *transportation*. Weathering is too universal and too well understood to warrant discussion here. In so far as plants play a part in it, it will be considered under "Reactions" (p. 83). A distinction between corrasion and transport is difficult if not impossible. With wind and water, the picking up of weathered particles involves carrying them as well, while gravity transports or affects transportation without picking the material up. In the beds of streams or glaciers, however, corrasion plays an essential part in freeing material for transport. Where some part of the rock is dissolved in the water, in the process of *corrosion*, the distinction from transport is also very slight.

As a rule the agent that picks up the material is the one which transports it, as is evident in the erosion of a gully or the scooping out of a sand-hill or dune. Often, however, material freed by gravity, as in talus slopes, is transported by water or wind. The distance of transport varies within the widest limits. In residuary soils the conversion of the rock takes place by weathering alone. Loosened material may be carried a few millimeters into the cracks of rocks, or it may be carried hundreds of miles and into totally different habitats and regions. The distance of transport naturally determines the place of deposit, but it will suffice to consider the latter alone.

Agents of erosion.—The great agents of erosion at the present time are water and wind. The action of ice, while of paramount importance during the glacial period, especially in transport, is now limited and local. The effect of gravity, combined with weathering, is less extensive than that of wind and water, but the areas so produced are of great service in studying succession,

owing to their number and relatively small size. Of topographic agencies, volcanoes alone produce no erosion, unless the violent removal of portions of volcanic cones be regarded as such.

In erosion, agents usually act alone, though it is often the case that one agent will erode an area deposited by another. It is true that water and gravity are regularly associated in erosion by water, but gravity is hardly to be regarded as controlling, except in the disintegration of peaks and cliffs, and in the case of avalanches, whether of snow or of rock and soil.

Rate and degree of erosion.—While the force and duration of the chief eroding agents, water and wind, differ greatly, they are critical in determining the rate of erosion and the degree to which it will act. These are also affected in the first degree by the hardness and compactness of the surface acted upon, as is shown by the formation of boulders and ledges in rock strata. The erosive force of rain-water depends upon the rate of precipitation and the angle of slope, that of running water upon the fall or current and the load carried. While these vary in all possible degrees, the essential fact is that they are more or less constant for a particular area. In many areas they are susceptible of approximate measurement and expression, at least. The erosive force of wind is determined by the velocity and by the exposure of the slope acted upon. Prairies and plains, deserts, ridges, mountain peaks, and shores are the chief areas characterized by forceful winds. Apart from velocity and exposure, the erosive influence of wind is determined by the length of the period for which it acts and the frequency of such periods. Certain areas, sand-hills, dunes, strands, and mountain-tops, for example, may have winds forceful enough to pick up sand or dust, every day for all or most of the year. In the case of compact soils or rock surfaces the action of the wind is confined to removing weathered material, unless the wind carries a load of abrasive particles.

In the case of water erosion, intensity often compensates for lack of duration or frequency, especially where the slope is great and vegetation scanty. This is especially true of regions with torrential rains, such as the deserts of the Southwest and the Black Hills and Rocky Mountains, where the characteristic "bad lands" occur. The density or hardness of the eroded surface, its roughness, and the amount and kind of dead or living cover, together with slope and exposure, are all factors of moment in determining the final effect of erosion. These are factors which permit of quantitive study with a minuteness and thoroughness not yet attempted. Such study seems inevitable if we are to make an accurate analysis of the forces which influence migration and occupation, and direct the water-content basis of successional development.

Fragmentary and superficial erosion.—Erosion may act over the whole surface of an area with greater or less uniformity; it may be restricted to particular portions or localized in the most minute way. Striking illustration of this is found in the comparison of ridge and slope with valley. Moreover, while the contrast between slope and valley is of the greatest, similar slopes exhibit similar or identical behavior. Marked examples of local erosion by wind are found in the blow-outs of sand-hills and dunes, while sand-draws and washes furnish similar cases of water erosion. Fragmentary erosion is a feature, however, of lateral erosion by running water, and of cliff and ridge erosion due to gravity. It furnishes a bewildering array of areas of all sizes

and degrees, which present wide conditions for ecesis. For this reason it offers material of the first importance for reconstructing the course of succession and relating the various stages. Superficial erosion to varying depths is likewise a ready source of developmental clues. When produced artificially under control, both processes furnish an invaluable experimental method of studying succession by denuded quadrats and transects (plate 3 A).

Bare areas due to water erosion.—The important areas laid bare through erosion by water are: (1) gullies, ravines, and valleys; (2) sand-draws; (3) washes; (4) flood-plains and river islands; (5) banks; (6) lake-shores and sea-shores; (7) crests and slopes; (8) bad lands; (9) buttes; (10) monadnocks. In some of these, such as stream-banks, the erosion is chiefly or wholly lateral, and hence more or less local and fragmentary. In others, *e. g.*, washes and flood-plains, the erosion is superficial and general, and is often intimately associated with deposition. The majority of them are the result of interaction of both methods, as illustrated in the production of a gully or ravine or a sea-shore. Bad lands and beaches represent, perhaps, the extreme conditions of erosion, in which colonization is all but impossible. In all, the success of initial invasion depends upon the kind of surface laid bare and the water-content as determined by the surface, the slope, and the climatic region. The form and nature of the area itself are important only as they affect these factors.

Bare areas due to wind erosion.—The most characteristic areas of this sort are wind-denuded areas of dunes and sand-hills, particularly the well-known blow-outs. Related to these are the strands from which the dune-sand is gathered by the wind, and the plains of rivers, lakes, and glacial margins from which sand-hills and loess deposits have been formed by wind action. Wind is a powerful factor in the erosion of strands, but at the present it is of slight importance in flood-plains and lacustrine plains as compared with its action in Tertiary and Quaternary times. The abrasion and removal of material from exposed peaks, ridges, and slopes of rocks is constantly going on, but it does not often assume such striking proportions as are seen in the characteristic mushroom rocks found in the Rocky Mountains. It plays some part, and often a controlling one, in the lichen and moss stages of the rock succession (plates 1 A, 2 B).

Bare areas due to gravity.—Many areas owe their origin to the action of gravity on material freed by weathering, or in some cases by water erosion. In the case of mountains, relatively large areas are exposed by exfoliation, crumbling, or slipping. In certain mountain regions with heavy snowfall, the effect of gravity on the snow-fields produces numerous characteristic snow-slides in which the ground is often swept bare. Crumbling and slipping are also universal processes on the steep slopes of crests and hills, and along stream-banks and lake and sea shores everywhere. From their hardness, instability, or dryness, and the steep or vertical faces, such areas are among the slowest to be invaded as a rule. In consequence, they often permit the persistence of initial stages or their recurrence long after they have disappeared elsewhere (plate 3 B).

Bare areas due to ice action.—At the present time, the effect of ice in producing bare habitats is confined to wind-exposed shores and to the margins of glaciers. In the latter case the final condition of the area is naturally due

in large degree to fluvial action as well. During the glacial period erosion of the hardest rocks or of softer materials to great depths was the universal accompaniment of glacial movement. In the Rocky Mountains and Sierra Nevada the extreme conditions which rock invaders must meet are often the direct outcome of glacial scouring in the past.

The action of wind-driven ice on exposed shores is a striking feature of many lakes in Minnesota and Wisconsin as well as elsewhere. Shores otherwise similar are differentiated by the grinding and pushing action of the ice. Bare shores are modified in various ways, while those covered with vegetation are denuded more or less completely (plate 3 c).

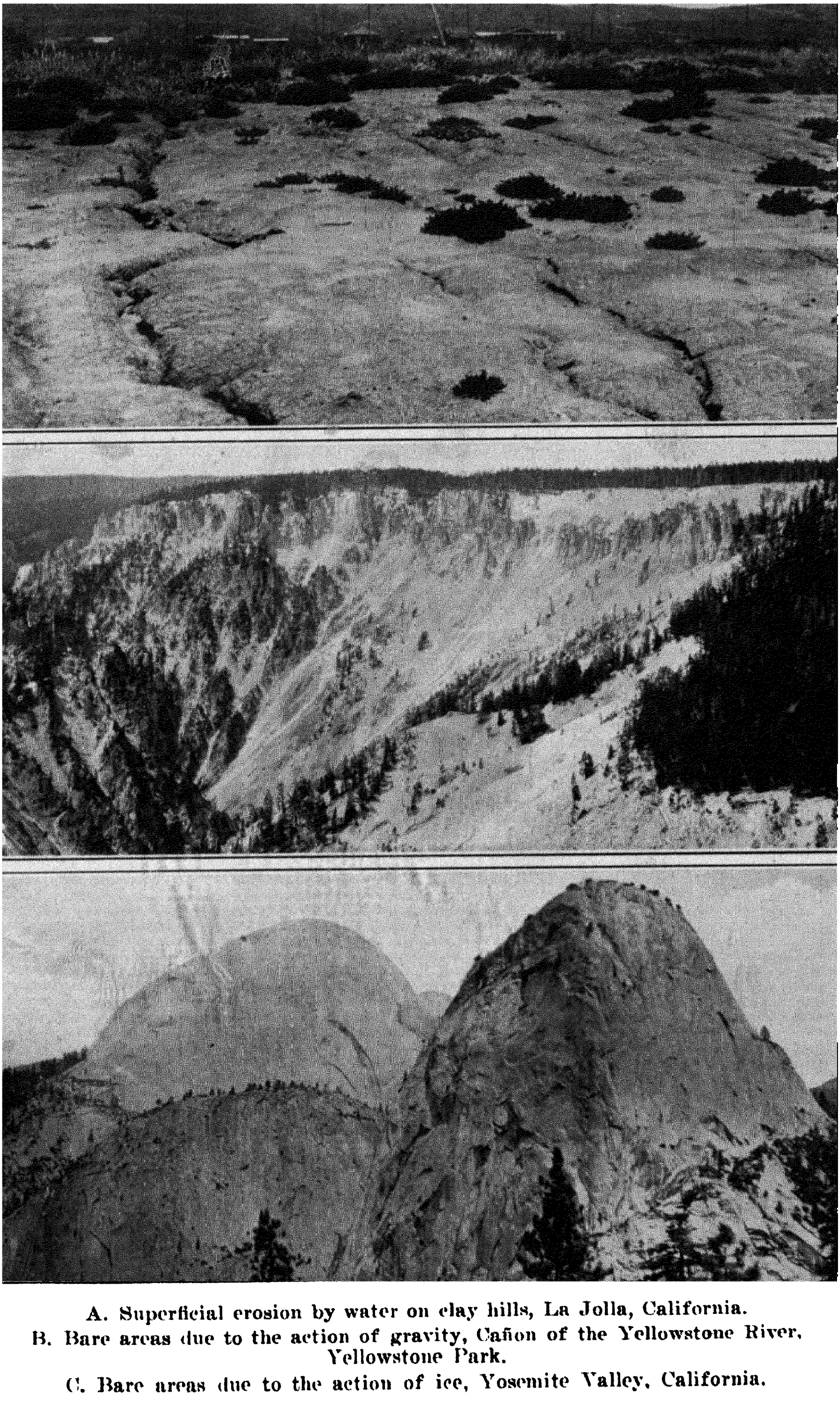
DEPOSIT.

Significance.—Deposit is such a regular and often such an immediate consequence of erosion that it is desirable to emphasize the fact that this essential relation, which is so fundamental to physiography, is of little or no consequence in the development of vegetation. Material eroded in one part of a drainage basin must in the usual course be deposited in another part, and in both cases it bears a direct relation to the development of the river system. This would be in no wise true of the development of the vegetation in the two areas, especially if the latter were in different climatic regions. Even in the same climatic region it is true only of final or subfinal stages. This latter fact, however, indicates no essential relationship, since all initial causes in the region give rise to seres which reach the same climax. It must also be recalled that the great deposits of marl, peat, travertine, sinter, and volcanic dust bear no relation to a preceding erosion.

The relation of deposit to the future development of vegetation depends upon a number of factors. These are: (1) the agency of transport; (2) kind of material; (3) manner of deposition; (4) rate, depth, and extent; (5) place and distance of deposit. These determine the rate at which the sere can develop, the physical conditions which the invaders must meet, the climax vegetation from which they can be drawn, and the effect of migration.

Agents of deposit.—If the term is used in the inclusive sense, the agents of deposit are: (1) running water; (2) ground-water; (3) wind; (4) glaciers, ice, and snow; (5) volcanoes; (6) gravity. Plants and animals also build deposits, but these are naturally considered under biotic agencies and under reactions. Just as it is practically impossible to draw a line between the loosening of material and its transport, so it is often equally impossible to separate transport from sedimentation. In any area of deposition the two are going on simultaneously, the dropping of part of the load carried by water, for example, permitting the further transport of the remainder. Deltas and alluvial fans are especially fine examples of the sorting due to the interaction of these two processes. They make it clear that any unit deposit is due to the varying distances of transport of the particles, as well as to the fact of their fall. However, in the case of a single particle, it is evident that this is first transported and then deposited, after which it may be transported and deposited again and again. In the study of a sediment actually forming, the last phase of transport must be included in deposition.

As is true of erosion also, two agents may interact in effecting deposition. The ordinary relation between two agents is successive, as in the case of



A. Superficial erosion by water on clay hills, La Jolla, California.
B. Bare areas due to the action of gravity, Cañon of the Yellowstone River, Yellowstone Park.
C. Bare areas due to the action of ice, Yosemite Valley, California.

beach-sand thrown up by the waves and finally deposited as dunes by the wind, or in the probable wind formation of loess from water-laid plains. In many cases, however, the action of the two agents is more or less simultaneous. This is especially true of the fluvio-glacial deposits due to the combined action of water and glaciers, and of beaches formed by the action of wave-borne ice. It is peculiarly characteristic of the deposits formed by ground-waters in surface streams, though here we are really dealing with a single agent, as is essentially true also in the case of snow-drifts due to wind. As to volcanoes, eruptive activity is the one agent concerned in lava-flows and cinder-cones, but this is combined with wind to effect the transport and deposit of volcanic dust.

Manner of deposit.—This depends upon the kind and nature of the agent and upon the kind of material. Ground-waters carry material in the finest condition, since it is in solution, and hence such deposits as sinter and travertine are the most uniform of all in composition and texture, if certain characteristic irregularities of surface are disregarded. Such deposits owe their uniformity and density, moreover, to the fact that the water contains cementing material alone, so to speak, while in the case of surface-water the solid particles are in much larger quantity than the material in solution. Winds also carry particles of a small range of size, and the resulting deposits are essentially homogeneous. As a consequence of the lack of cementing material in solution, dunes, sand-hills, masses of volcanic dust, etc., are also characteristically unstable. An exception to this is furnished by loess, though the stability here is perhaps due to the later cementing action of absorbed water.

Water and ice exhibit the widest range in the size of the materials carried and in the amount of cementing action present. This is of course particularly true of glaciers. They show the most striking difference in the sorting of materials, moreover, as is well known. Lateral sorting is practically absent from true glacial deposits, while it is typical of water sediments. Glacial deposits possess much less cohesion in consequence of this fact and of the wider range in the size of particles, but also because of the greater lack of cementing substances.

The nature of the solid particles and of the cementing materials is also a determining factor in the hardness of the deposit. While an uncemented deposit is ready for invasion as soon as water conditions warrant, sedimentary rock must first be weathered before it will permit penetration or possess the requisite water-content. Rocks cemented by lime respond most readily to weathering processes, though many exceptions are produced by differences in the amount of cement, quite apart from its nature, and also by pressure and metamorphism. Differences in the material of the particles, as between sand and clay for example, are controlling as to the holard and echard, and are consequently decisive in the ecesis of pioneer migrants.

Rate and depth of deposit.—The rapidity with which a deposit accumulates depends upon the amount of material carried, upon the duration or frequency of the agency, and upon the barrier to movement which effects the deposition of the load. The rate of deposit is of importance in determining the rate at which vegetation is overwhelmed and at which the deposit will reach a point where colonization will be possible. It also affects the reactions of the early stages of succession, as well as the period of each. These

are often more directly related to the continuous or intermittent nature of the deposition than to the rate itself. The depth of the deposit is chiefly an effect of the rate and duration, but it also has to do with the area as well, a fact axiomatic of lowlands (plate 4 A).

Place of deposit.—The place of deposit is critical for two reasons: (1) it controls the water conditions of the new area, and (2) it determines the climatic area and the climax formation in which the new sere will develop. Places of deposit fall into two distinct groups, namely, (1) in water, (2) on land (plate 4). These differ primarily, and sometimes only with respect to the extremeness of conditions as to colonization. Deposits in water must be built up to a level at which submerged plants can ecize before the sere proper begins, a process which is often a matter of centuries and ages. They can be invaded only by water-plants, and the early stages of succession are often very long. Deposits on land, however, can be invaded at once. The physical conditions are necessarily further from the extreme, a wider range of life-forms can enter as pioneers, and the stages of development are usually fewer and shorter.

Deposit by water is regularly in water, except in such cases as surface wash, but the withdrawal of flood-waters produces what is essentially a deposit on land. Aeolian deposits, on the contrary, are mostly on land, primarily because the material composing them is picked up from beaches and flood-plains by winds blowing from the water area. In the case of dunes, however, they may be carried into lakes, ponds, and swamps, and initiate a sere widely divergent from that on the dunes proper. The course of successional development also depends upon deposition in salt water, fresh water, or alkaline water. Water deposits may be changed into land areas by drainage and elevation, and the land deposits into water deposits in vegetational effect by flooding and subsidence. The elevation of water deposits has naturally been a chief initiating cause of the great eoseres of the geological past. Gravity deposits occur with equal readiness and in countless numbers along sea-coasts, lake-shores, and stream-banks, and in all hilly and mountainous regions. Along shores they are in land or water or both; in the case of hills and mountains they are typically land deposits. Glacial deposits produce both land and water areas, though they are first actually laid down in water as the ice melts. The same is true of fluvio-glacial deposits, though these necessarily show more relationship to water deposits.

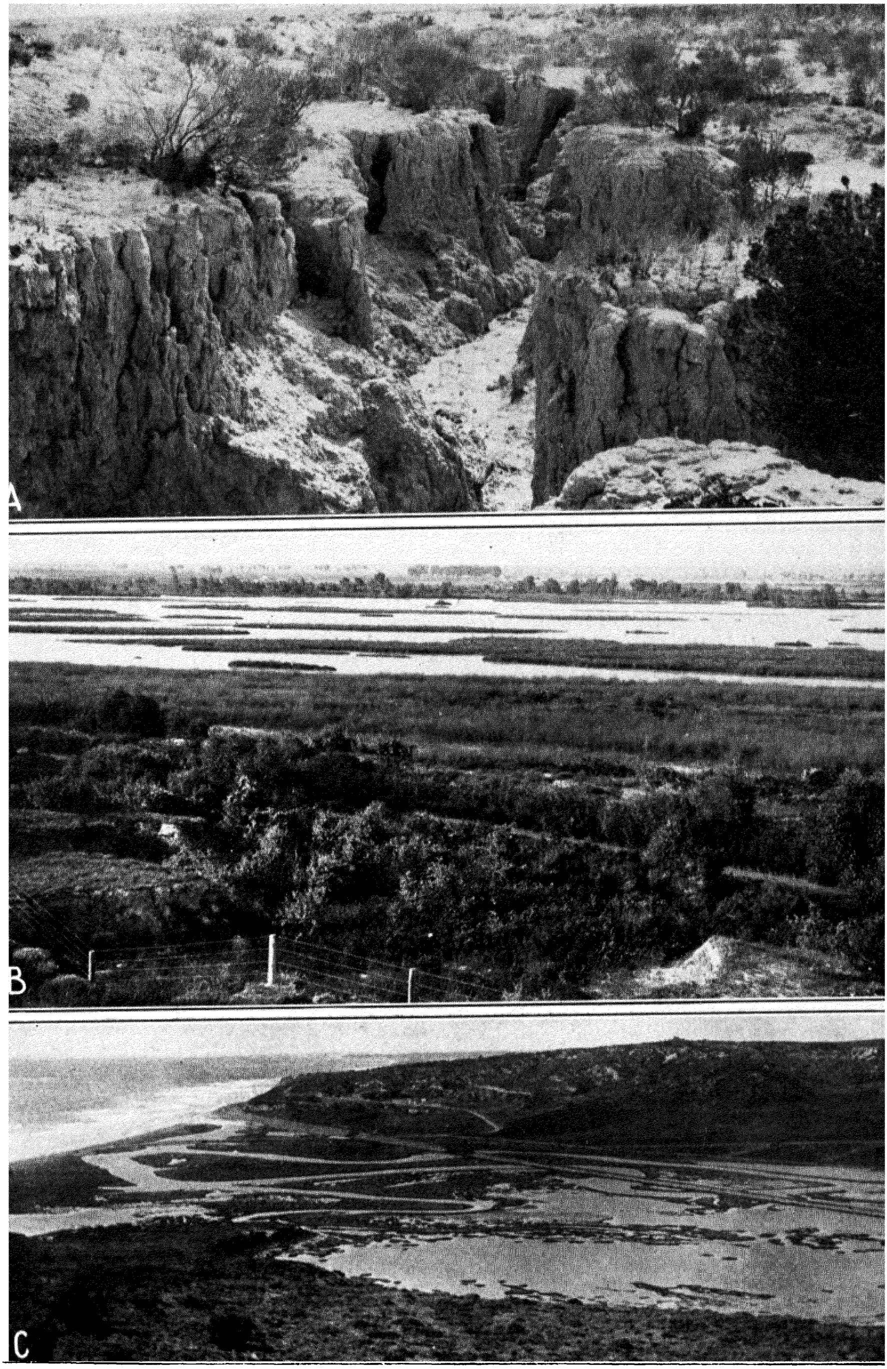
Distance of transport.—Transported material is deposited at every conceivable distance from the place of origin. It may be washed by water or blown by wind into a crack a few millimeters distant, or it may be carried thousands of miles and find its resting-place on the bottom of the ocean. Water deposits may be found at the greatest distance from their source, and glacial deposits come next in this respect. The range of wind deposits at the present day is much less, while deposits due to volcanoes, ground water, and gravity are local. Distance naturally effects no sharp distinction between deposits, but it is a factor to be considered, especially in the relation of the new area to migration and to climax vegetation. From this point of view it is profitable to distinguish (1) deposition in the minor community where the material originated, (2) in other communities of the same climax association, (3) in areas controlled by earlier stages of a sere, but in the same climatic

region, (4) in another climatic region, and hence another climax formation. As is at once evident, the point of initiation, the course of development, and the final climax all hinge upon the effect of distance.

Fragmentary and local deposit.—As has just been seen, deposits may be local, as well as of extremely small area. The clearest examples of this are to be found in weathered rocks, cliffs, and ledges, where deposit occurs in tiny cracks, in clefts, or in large fissures. Here the deposit is often so slight that the plants growing in it seem to be growing on rock, and hence to belong to the initial stage of the rock sere. A careful scrutiny shows that they are not true rock-plants, comparable with lichens and mosses, but that they are soil-plants, or in some cases water-plants. Local deposit in small separate areas, like local erosion, produces innumerable small communities, each with its proper place in the sere, but often so surrounded or interrupted by plants of other stages that great confusion results (plate 4 A). In much work that has been done upon succession so far, the course of development, the movement of the population, and the relationship to the physical factors have been lost or confused by the failure to recognize how detailed and accurate this scrutiny must be. As is shown later in full, only the use of exact quadrat and transect methods can show the way in such cases.

Sterility of deposits.—Deposits vary greatly in the numbers of disseminules found in them, a factor of considerable importance in the development of the first stages. The number of viable propagules depends upon the source of the material as well as upon the agent. The deposits of wind-borne volcanic dust and of sinter and travertine formed by ground-water represent the one extreme of almost absolute sterility. Primary dune-sand, *i. e.*, blown more or less directly from the beach, probably comes next, while secondary dune-sand from established dunes would contain more seeds and fruits. Glacial deposits are sterile, though terminal and lateral moraines of existing glaciers are relatively an exception. Water deposits contain disseminules in varying numbers, but for the most part they are relatively rich, though the viability of many of the seeds is usually low. Talus deposits, land-slides, etc., tend to contain the maximum number of seeds and fruits, owing to the fact that plants and plant parts are so often carried down with the falling material, and to the favorable conditions for the preservation of seeds in a viable condition.

Bare areas due to deposit by moving water.—Under this term are included (1) streams and run-off and (2) waves, tides, and shore-currents. The typical areas of deposit by running water, which includes streams of all degrees as well as surface run-off, are the following: (1) alluvial cones, fans, bajadas, etc.; (2) alluvial plains; (3) flood-plains; (4) channel deposits; (5) deltas; (6) beds of lakes. Topographically, the first three are much more closely related in the essentials of the process of formation than their names indicate. It is practically impossible to distinguish between an alluvial plain and a flood-plain, if they are not indeed identical. Alluvial cones and fans often merge into a complex, which is called by Salisbury (1907:183) a piedmont alluvial plain. It is clear that the sand-bars of a river differ in little but form from the deltas made in it by lateral streams, and in the case of a braided river such as the Platte, the different streams of the network may form deltas, lateral banks, and median bars in the same channel. More-



A. Local and fragmentary deposit in a young ravine, bad lands, Scott's Bluff, Nebraska.
B. Sand-bars due to deposit in streams, North Platte River, Scott's Bluff, Nebraska.
C. Silting up of the Soledad Estuary, La Jolla, California.

slowly weather the surface and collect organic material for later stages. Salt may be deposited from spring-waters, as in salt basins, or by the water of lakes in arid regions where evaporation exceeds the inflow. In moist and semi-arid regions the salt crust is usually thin, and hence readily dissolved or weathered away, permitting halophytes to enter and begin the succession. In arid regions, on the contrary, the deposits are thicker, and removal by weathering or solution is nearly impossible, so that extensive areas in Utah and Nevada remain absolutely sterile under present conditions.

Bare areas due to deposit by wind.—The principal wind deposits are (1) sand, chiefly in the form of dunes; (2) loess; (3) volcanic dust. Of these, dunes, both inland and coastal, are much the most important at the present time. Loess, while covering enormous areas in the valleys of the Mississippi, Rhine, Danube, Hoang-Ho, and other rivers, is not in process of formation to-day, and the prisere developed upon it can not now be traced in the actual course of development. Deposits of volcanic dust are infrequent and localized, and cover relatively small areas. They are unique in the suddenness and completeness with which the area is covered and in their absolute sterility.

Dunes are classical examples of deposits which initiate succession. Their wide distribution and striking mobility have made them favorite subjects of investigation by both physiographer and botanist, and there is probably no other initial area and succession of which we know so much. In spite of their characteristic topography, however, dunes affect succession by virtue of instability and water relations, and not by form. This is shown by the inland dunes or sand-hills of the Great Plains. Hills, deep hollows or blow-outs, and sandy plains show the same development, regardless of their differences of form. In all of these the controlling part is played by the sand-catching and sand-binding plants, usually grasses, which act as pioneers. The chief reactions are three, namely, fixation of the sand, gradual accumulation of humus, and decrease of evaporation and increase of holard (plate 1 A).

Dune plants have often been regarded as halophytes, but since Kearney (1904) has shown that this is rarely true of strand species, it seems impossible to distinguish initial dune areas on the basis of salinity. This is borne out by the similarity of the early stages of shore dunes, whether lacustrine or marine. As a result of their location these often differ much in the later stages, and especially in the climax. Inland dunes occur in widely different climatic regions and differ from each other in population as well as from coastal dunes. This is well illustrated by the sand-hills of Nebraska, the "white sands" of southern New Mexico, and the barchans of Turkestan.

Deposit by ice and snow.—Of these agencies, glaciers have been of much the greatest importance in the past, though their action to-day is localized in mountains and the polar regions. The effect of shore-ice, though interesting, is rarely sufficient to produce a distinct result. The influence of snow is often striking and decisive, but it is also peculiar to mountain regions. Naturally, all of these show a close dependence upon water, as is seen in the water relations of the resulting soils.

Bare areas due to deposit by glaciers.—From the standpoint of succession there is no essential difference between glacial and fluvio-glacial deposits. This is readily explained by the fact that glacial materials are really deposited in water at the time of general melting. The effect upon the new soil is prac-

tically the same as when it is water-laid after being carried for some time from the glacier. In the case of drumlins, indeed, it seems probable that they may be due either to fluvio-glacial deposits or to erosion by an ice-sheet of an antecedent ground-moraine. Hence it seems immaterial whether the deposit is glacial, *e. g.*, lateral and terminal moraines, ground-moraines, or drumlins, or fluvio-glacial, such as valley trains, outwash plains, eskars, kames, or drumlins (plate 5 A).

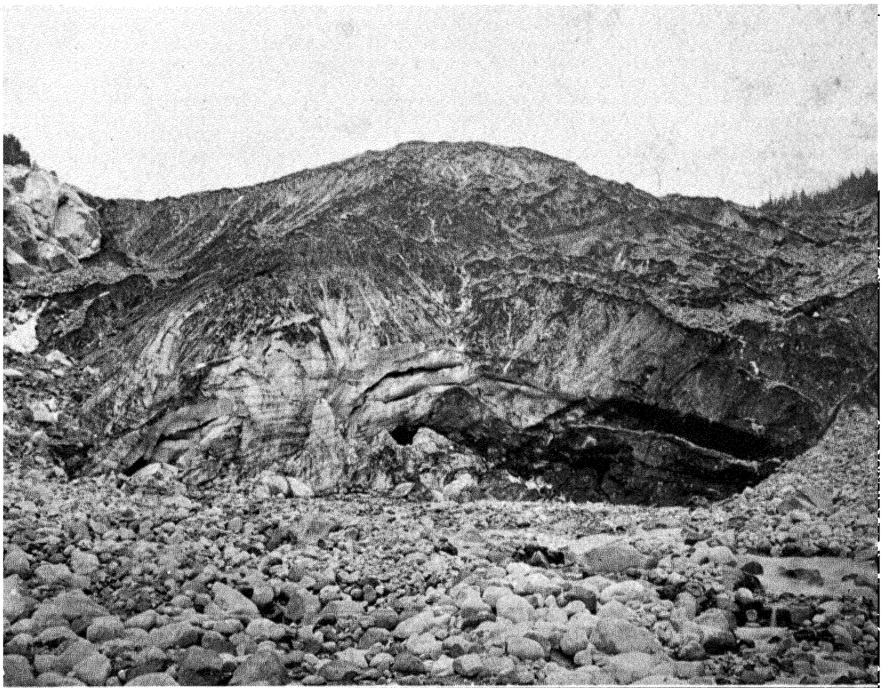
The essential effects of glacial deposition are produced by the size and uniformity of the particles and by the place of deposit, *i. e.*, on land or in water. While fluvio-glacial deposits often show more sorting, glacial soils proper show all possible variations. A till sheet may consist of gravel, sand, or clay, but frequently of all three. It may contain pebbles, or boulders, or the deposit may be largely made up of enormous blocks. The latter present the extreme conditions for rock succession, while the till sheet proper offers an area prepared for a higher type of colonists. The ratio of sand or gravel to clay determines the holard and echard of the till and the invasions upon it. This is relatively immaterial when deposit occurs in water, but is significant in the ordinary case of deposit on land, particularly where there is considerable initial relief. Here the influence of slope upon water from the melting ice is the same as upon ordinary precipitation. The ridges are drier, valleys wetter, and the slopes intermediate, and the course of succession varies accordingly.

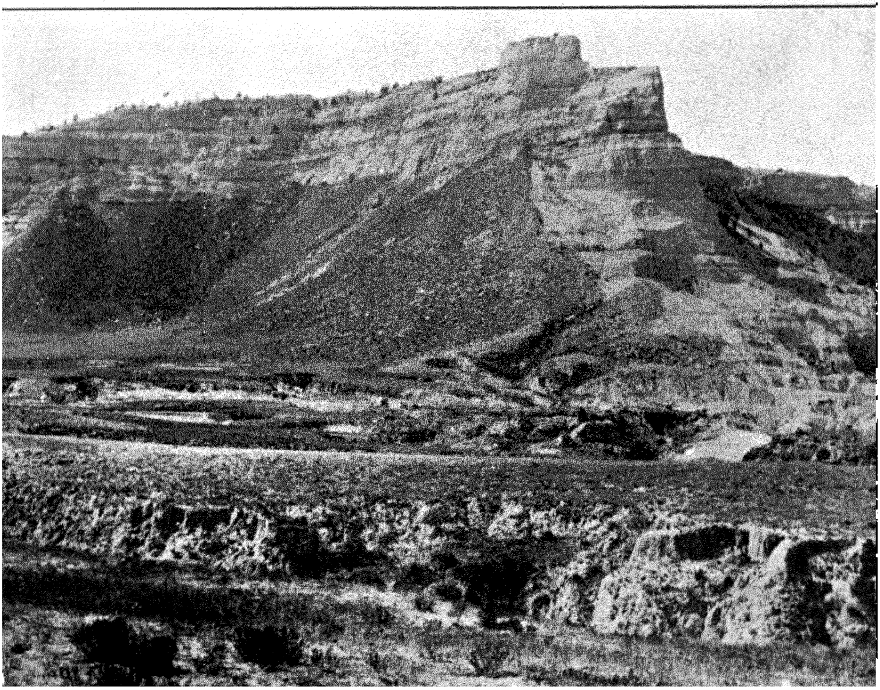
Bare areas due to deposit by ice and snow.—The action of shore-ice is a combination of erosion and deposit, though when a shore-wall is thus formed it is a true deposit. Its structure, depth, and extent usually distinguish it but slightly from the ordinary shore. In consequence, the development of vegetation upon it rarely produces any distinctive features.

Deposit in consequence of snow action is confined to snow-slide masses and to flat areas or hollows in which snow melts. In such snow-hollows the deposit is usually insignificant, but the accumulation of the dust and sand brought to the snow-field by wind often becomes appreciable in a few years. In practically all cases the real effect is produced by the partial destruction of vegetation by the snow and the ponding of the snow-water.

Snow-slides may be assigned either to snow or gravity, since they are due to the combined action of both. They are more frequent than land-slides of like extent, but they differ from them in few respects. A snow-slide sweeps away the vegetation more or less completely, but may disturb the soil to a slight depth only. A heavy fall of snow may initiate a land-slide, however. The mass of detritus at the bottom of a snow-slide is much more homogeneous and contains more plant material than do most land-slides. It differs also in the fact that it may require one or more summers for the snow to melt. During this time the mass remains cold and wet, and invasion is correspondingly slow.

Bare areas due to deposit by gravity.—Talus masses and slopes are universal deposits at the base of cliffs, shores, banks, etc. From the nature of their formation they differ chiefly in composition, apart from differences due to location. The initial conditions presented are often very like those of the cliff or bank above. The chief change is one of density or coherence. This is well shown by the fact that the lichens and cleft plants of a granite cliff or wall are usually found in the talus as well, even when this shows the degree of disintegration found in a gravel-slide. Rock talus, in consequence, really





A. Terminal moraine of the Nisqually Glacier, Mount Rainier, Washington; bare area due to deposit by a glacier.

B. Talus slopes of Scott's Bluff, Nebraska; bare areas due to gravity.

continues the pioneer stage begun on the fragmenting area. The development is hastened by the more rapid weathering and the greater irregularity of surface, which permit corresponding variations of holard. Talus derived from soils such as sand or clay, or from rocks which decompose readily, presents typically more extreme conditions as to water-content and stability than the fragmenting area. The initial stages upon talus are hence new stages, and show much less relationship to the population of the top of cliff or bank (plate 5 B).

The location of the talus is important in determining its water relations, as well as its possible population. Along banks that are being undercut, the material is swept away, but when the current leaves the shore the talus is often built up in the water. This happens not infrequently on lake-shores as well. In both cases the excessive holard which results initiates the succession with a hydrophytic or amphibious stage. When the talus accumulates on land, as is the rule, the initial holard is typically less than the normal for the particular soil in the climatic region concerned. This arises from the looseness and unevenness of the talus and the corresponding ease of evaporation from the soil. In desert regions this tendency becomes decisive, and the colonization of the south and west slopes is extremely difficult.

Bare areas due to volcanic deposits.—Volcanic agencies bring about deposits of lava, of cinders so-called, of ash or dust, and of sinter. Deposits of ash have already been considered briefly under "Wind." The local deposition of ash is less influenced by wind, and the depth of accumulation is often very great, sometimes reaching 50 to 100 feet. On the cones themselves it is frequently much greater. Coarser material—cinders, rocks, and enormous stones—are also blown from craters in great quantities and fall near the cone or upon its slopes. The lava and mud expelled from volcanoes flow in streams from the crater. Rivers of lava have been known to reach a length of 50 miles and a width of half a mile. In flat places the stream spreads out and forms a lava lake which hardens into a plain. Mud volcanoes are small, geyser-like structures which discharge mud. They build up small cones, which are usually grouped and cover considerable areas with their deposits. The deposits due to volcanoes or geysers regularly result in the destruction of vegetation, but this effect may be produced alone, as a consequence of the emission of poisonous gases, steam, hot water, or hot mud, of fire-blasts or the heating of the soil. Such bare areas are characteristic features of Yellowstone Park.

All volcanic deposits are characterized by great sterility. They are usually small in extent, and hence easily accessible to migrants. The ease of invasion depends largely upon the coherence of the deposit. Invasion takes place more readily in ash and cinders than upon lava, unless they are quite deep. Mud deposits would apparently be invaded most readily. The seres of volcanic deposits have been little studied, but it is known that they are relatively long. As would be expected, this is particularly true of lava, though climate exerts a decisive effect, as is shown by the invasion of lava fields in Iceland and Java.

Ponding and draining.—These constitute a second pair of related but opposite topographic processes. Flooding or ponding is almost inevitably followed by draining, and the drainage of an area may be obstructed and

result in flooding at almost any time. Ponding usually produces extreme water conditions, with a corresponding effect upon succession. Drainage reduces the depth of water, or extreme holard, and accordingly shortens the development. Although opposite as processes, the two may produce exactly the same initial area. This is probably a frequent occurrence. Ponding may be so shallow as to permit the immediate entrance of hydrophytes or of amphibious plants. Drainage may reduce the level of pond or lake without completely emptying it, and thus produce similar depths for invaders. Here again it is evident that the water relation of the new area is decisive, and not the originating process.

Kinds of lakes and ponds.—Lakes and ponds have been classified from many points of view, such as form, origin, physiographic development, chemical nature, climatic region, depth, duration, etc. All of these bases have some relation to succession, though this seems least direct in the case of physiographic development and manner of origin. The amount and kind of water are the controlling factors in determining when the pioneer stages of a sere can develop, just as the extent and location determine the pioneers and the rate at which they can invade. Depth, as modified by evaporation, filling, and draining, is the critical point upon which invasion turns. Depth, extent, and kind of water are unimportant points to the geographer, however, and his classification can not be expected to reveal basic vegetational values. It does, however, bring out many points which the ecologist must note in connection with water and soil relations. The classification proposed by Russell (1895) perhaps serves this purpose best because of its detail. The agencies of lake and pond formation are grouped as follows:

1. New land depressions.
2. Atmospheric.
   (1) Wind rock basins.
   (2) Dune ponds.
3. Aqueous.
   (1) Streams.
      (*a*) Excavation and change of bed.
      (*b*) Lateral deltas and valley cones.
      (*c*) Ponding of tributaries.
      (*d*) Ox-bows or cut-offs.
      (*e*) Delta lakes.
   (2) Waves and currents.
      (*a*) Bar lakes.
4. Glacial.
   (1) Damming of laterals by ice.
   (2) Damming by drift.
   (3) Scouring.
5. Volcanic.
   (1) Damming by lava.
   (2) Damming by ash.
   (3) Crater lakes.
6. Meteoric?
7. Earthquakes.
8. Organic agencies.
   (1) Coral?
   (2) Peat moss.
   (3) Beaver dams.
   (4) River rafts.
   (5) Gas mud-holes.
   (6) Wallows.
9. Diastrophic.
10. Land-slides.
11. Chemical action.
12. Interaction of two or more agents.

Life-history of a lake.—While the relation of a lake to its river system seems to have no significance for succession, it is evident that the life-history of a lake shows a direct relation. A lake in a humid region matures by filling with detritus, by the cutting down of its outlet, by the shallowing action of plants, or by the combined influence of these processes. When the depth is reduced to a few meters, pioneer hydrophytes appear. From this point the maturity and depth of the lake and the succession of the vegetation are but different aspects of one complex process. At any time in this process the lake may be rejuvenated by an increase of the water-supply, by the damming of the outlet, or by the sinking of the basin. All of these have the same effect,

namely, that of increasing the depth of the water. The vegetation is wholly destroyed if the depth increases more than a few feet in the early stages of the sere, or even a few inches in later grassland and woodland stages. A new sere of the same succession is initiated as soon as the water is again shallowed to a point where submerged hydrophytes can ecize. The significant fact is that the development of the sere in the original and in the rejuvenated lake will be essentially or wholly identical. Physiographically, the two lakes are essentially different. As initial areas for succession, they are identical.

In the case of a lake in an arid region, evaporation is the chief factor in shallowing, though filling by detritus plays a part. The cutting down of the outlet is of little or no importance, owing to the reduction in volume. The shallowing effect of vegetation can be felt only in relative youth, as the increasing salinity destroys the plant population. Hence, the development of the usual water sere ceases long before the death of the lake, in such bodies of water as Great Salt Lake for example. Consequently there is no correspondence between the life-history of the lake and the development of the vegetation. Instead of a drying lake-bed, densely clothed with plants, the salt-incrusted bottom is entirely devoid of vegetation. In an arid climate it is only after many years that the salt crust is sufficiently destroyed by solution and removal to permit the appearance of pioneer halophytes. If a striking increase of rainfall or the accession of new streams should rejuvenate the lake, the initiation of a sere would depend largely upon the freshness of the water. If vegetation does appear its development will be determined by whether the water remains fresh or is renderd saline by evaporation.

In the case of periodic ponds, playa lakes, etc., the drainage is usually such as to prevent the accumulation of solutes. The life of the pond is often short, and hydrophytic vegetation may fail to develop altogether, the sere beginning on the exposed, rapidly drying bottom. Ponds which last for several years permit more complete expression of the water sere. Salt ponds supplied by springs, such as the Salt Basin at Lincoln, are unique in behavior. They possess no phanerogamic vegetation at all, except when greatly diluted by fresh-water streams. Ordinarily they dry up, forming a salt crust, as in the lakes of arid regions. The periodic ponds of the Great Plains also deposit alkali when they evaporate, though this is often not so great in amount as to prevent the invasion of halophytes. The latter initiate a short succession which terminates in the climatic grassland.

Drainage.—Drainage by cutting down the outlet of the lake or pond plays some part in shallowing most lakes of humid regions. It is usually subordinate to filling, and in effect is indistinguishable from it. As an initial cause of new areas for succession, it is most evident where natural barriers which produce ponding are suddenly removed, and especially where it is resorted to intentionally by man. The effect of drainage upon the course of development is determined by the degree to which the water is removed. If open water with a depth not greater than 12 meters is left, the normal water succession is initiated. Later stages are initial at the respective depths less than this, until a point is reached where drainage completely removes the surface water. This permits the soil to dry more or less rapidly and to become quickly covered with a growth of mesophytic ruderals or subruderals. This is typically the case in areas drained artificially.

The effect of drainage is perhaps most striking when the level of the lake is reduced to a point where islands and peninsulas appear. The rate of lowering determines the water conditions at which invasion becomes possible, and hence the presence and length of hydrophytic stages. In the behavior of a river-plain after flooding, draining differentiates the area into ponds and mud-flats, in which the water sere will appear in a variety of stages.

ELEVATION AND SUBSIDENCE.

Elevation and subsidence.—These are likewise examples of processes which are opposite and complementary in many instances. This is seen in the relation of syncline and anticline, in earthquakes, in the movements of certain sea-coasts, etc. Naturally they affect the development of the vegetation directly only where land and water are in contact. The relative rise or fall of an inland area could produce no effect upon succession, except as it changed the climate or produced flooding or draining. A direct effect upon vegetation is possible only along sea-coasts and lake-coasts, and of course upon islands. Here, however, the rate of emergence or submergence is the decisive factor. Physiographically, it is much the same thing whether a coast rises or falls a foot a year or in a thousand years. From the standpoint of succession, the rates of elevation and subsidence assumed for the Atlantic coast, the coast of Sweden, and for the Great Lakes are so slow as to be wholly insignificant. A rise of 2.5 feet in a century is equivalent to a rise of less than a centimeter per year. Over such a minute area as would result from such a rise each year, there would be no chance for extreme conditions and no place for even the most incomplete and fragmentary succession. Each annual increment of space would be controlled by the association at hand and quickly made an intrinsic part of it.

With subsidence the case is different if it results in flooding and consequent destruction of the vegetation. In the case of a low-lying coastal forest even the slow rate of 3 feet per century would eventually flood the forest floor and kill the trees. It is conceivable that the flooded forest floor might serve as a new area for the invasion of a coastal swamp, thus causing an apparent "retrogressive" succession. It seems much more probable, however, that the action of waves and tides would erode the soil, and thus destroy the forest or other vegetation piecemeal year after year.

While elevation and subsidence are largely negligible to-day as initial causes of succession, this is obviously not true of the past. Crustal movements were of the first importance in changing the outlines of continents, in building mountains, and in producing cycles of erosion. As a consequence of such changes they exerted a profound effect upon climate. The consequent effect upon vegetation resulted in the change of climax populations and in the initiation of a new cosere.

New areas due to elevation.—As assumed above, elevation produces new areas for succession only where it is relatively rapid, or where the new area is not in contact with an existing vegetation. Cases of this kind are practically confined at the present day to volcanic cones formed in lakes or in the ocean, to islands due to volcanic disturbances, and to coral reefs and islands. The latter, however, belong properly under biotic initial causes, though their formation and behavior are often intimately associated with volcanic islands.

Apparently no studies have been made as yet of the development of vegetation on new islands due to volcanic action. It seems evident, however, that they would exhibit rock and cinder seres generally, with the water sere of coral and other oceanic islands at the lowest level.

Subsidence.—The evidences for the recent subsidence of the Atlantic coast of the United States are summed up by Johnson (1913:451), as:

(1) Wholly fictitious appearance of changes of level; (2) phenomena produced by local changes in tidal heights without any real change in the general level of either land or sea; (3) phenomena really produced by a sinking of the land, but so long ago that they can not properly be cited as proofs of subsidence within the last few thousand years. The fictitious appearance of change of level is given by (1) standing forests killed by the invasion of the sea; (2) submerged stumps; (3) submerged peat. Lyall, Cook, Gesner, Ganong, and others have regarded dead standing forests as conclusive evidence of the subsidence of the Atlantic coast. Goldthwaite found that death resulted in some cases from fire and in others from a local rise in the high-tide level. Johnson ascribed three distinct causes for the death of the forests about Cascumpeque Harbor in Prince Edward Island. Accumulations of sand in the forest caused the ponding back of storm-waters, and the consequent death of the trees. Elsewhere, small waves had eroded the earth from the tree-roots and exposed them to salt water. Finally, the number and width of the inlets in the barrier beach had caused a local rise in the high-tide surface and a consequent invasion of the forest by salt water. The author explains the presence of live cypresses in water often over 5 feet deep by finding that the spreading bases were just above water-level at the same elevation as on the adjacent low shore, and that the submerged parts were really spreading roots. The trees had grown on a low coast composed of peaty soil, and the erosion of the latter by the waves had left the trees standing in water.

Submerged stumps are found to arise in a variety of ways independently of coastal subsidence. Along the shores of South Carolina and Georgia, small waves undermine the trees and let them down into salt water, often in the erect position. The trunks later break off at the water-line and leave upright submerged stumps. Similar stumps are also produced by the long tap-roots of certain trees, such as the loblolly pine. Submerged stumps, due to a local rise of the high-tide level, to the compression of peat-bogs caused by a lowering of the ground-water level as the waves cut into the shoreward side of such bogs, to the compression of deposits due to the weight of barrier beaches, as well as to many other causes, have been observed. It is also pointed out that beds of submerged peat containing stumps may be caused by the sinking of floating bogs, by the lowering of the ground-water and the consequent lowering of the surface of the bog when the latter is encroached upon by the sea, or by the weight of a barrier beach, compressing the peat so that it is exposed at or below tide-level on the seaward side of the beach.

The phenomena produced by a local rise in the high-tide level are explained in detail. A bay nearly separated from the sea by a barrier beach, but connected with it by a narrow tidal inlet, will have a lower high-tide level. Trees and other vegetation will grow down to the high-tide level of the bay, and hence below the high-tide level of the sea. Whenever a large breach is made in the barrier beach the high-tide level will become the same in the bay as for the sea. All trees whose bases are below this high-tide level will be killed and will later be represented by submerged stumps. The surface of the salt marsh will build up to the new high-tide level, enveloping stumps and other plant remains. Fresh-water peat may also be buried under a layer of salt-

marsh peat. Changes of high-tide level with the killing of forests have actually been observed, as near Boston in 1898, when a large opening was made in a barrier beach by a storm.

Appearances of subsidence predominate over those of elevation because marsh deposits tend to sink to the new level when the high-tide level is lowered because the immediate destruction of fresh-water vegetation by salt-water when the high-tide limit is raised is more striking than the slow recovery of marine areas by fresh vegetation when the high-tide level is lowered, and because in the cycle of shore-line development retrograding exceeds pro-grading, and retrograding tends to carry higher tide-levels into low lands, where apparent changes of level are most easily recognized.

The above conclusions have been given in some detail because there can be no question of the existence of fictitious evidences of subsidence. On the other hand, it is equally clear that existing subsidence would produce similar or identical phenomena, as Davis (1910:635) has well shown in the case of the layers of salt-marsh grasses. To the ecologist the actual facts of coastal seres and coseres are the important ones, upon which must be based the final decision as to the causal action of subsidence or of change of tide-level. It is clear, however, that slow subsidence, whether recent or remote, can only destroy amphibious or land vegetation and preserve the plants more or less completely in the form of peat as an evidence of former communities. It can not initiate a new area for colonization, except in so far as the ocean itself may be so regarded.

Earthquakes.—Practically no attention has been paid to the effects of earthquakes in producing new areas. It is obvious that a variety of different areas may arise from the action of earthquakes, either directly or indirectly. The direct effects are seen in the emergence of land from water and the subsidence of sea-coasts and deltas, and in the formation of small craters and mud-cones. Indirect effects arise in valleys where the drainage is disturbed by faults or otherwise, and new areas are consequently formed by ponding or draining. Earthquakes also loosen masses of rock or soil from cliffs and slopes, producing talus and slide masses. The great tidal-waves of earthquakes must also produce striking effects in denudation, erosion, and ponding on coast lands and islands in their path. An earthquake is thus a primary cause which has erosion, deposit, flooding, draining, elevation, and subsidence at its command in producing bare areas on which succession will occur.

Similarity of topographic processes.—The paired character of topographic processes has already been remarked. Erosion and deposit, flooding and draining, elevation and subsidence are all pairs of opposite and more or less related processes from the standpoint of topography (plates 2 A, 7 B). To the ecologist, however, they are alike in being initial processes which produce new or denuded areas for succession. From this viewpoint their similarity depends upon the water relations of the new area. Flooding and subsidence produce new water areas, draining and elevation new land areas. Gradual deposition in water makes the latter susceptible to colonization, while erosion exposes the land surfaces to invasion. Theoretically, at least, it is possible for all of these six processes to produce bare areas of essentially the same water-content within the same climax region, and hence to initiate the same succession. The shores of large lakes do actually exhibit the same water succession in initial areas produced by each of the four processes, deposit,

flooding, draining, and erosion. It would be altogether unusual for elevation and subsidence to be added to these, but it could at least happen in a region subject to earthquakes or volcanic disturbances. It must have occurred repeatedly in geological periods characterized by great diastrophic changes.

EDAPHIC CAUSES.

Nature.—In the preceding account of topographic processes which produce bare areas, it has frequently been shown that the critical results are the soil structure and the amount and kind of water-content. This is equally true of new areas due to climatic and biotic agents. In the case of all initial causes, therefore, the basic control is exerted by water-content, which is controlled in its turn by the physical character of the soil. A change in the kind of soil-water may seem an instance of an edaphic initial cause. The real cause, however, is topographic in the case of a change from salt to fresh water or the reverse, climatic in the increasing alkalinity of the lakes and pools of arid regions, and biotic when acid or other injurious substances accumulate in the soil. All seres are consequently more or less edaphic in nature, and hence the term edaphic can not well be used to distinguish one kind from another or to contrast with climatic causes. If seres are grouped in accordance with initial causes, they can be distinguished only on the basis of the forces which lie behind the changed conditions of soil and water. These are topographic, climatic, and biotic agents. In a developmental classification of seres such a basis is believed to be of secondary value. While such a grouping is simple and convenient, it is artificial because it ignores development, and because of the fact that very dissimilar initial causes produce identical bare areas and seres.

CLIMATIC CAUSES.

Rôle.—Climate may produce new areas for succession, or it may modify existing seres by changing the rate or direction of development, by displacing the climax, etc. As a cause of modification, the discussion of climate belongs elsewhere, and will be found in the chapters on direction, climax, and eosere. We are concerned with it here only as an initiator of new seres. In this rôle it acts usually through the agency of the ordinary changes and phenomena which constitute weather. A distinction between climate and weather is manifestly impossible. It is clear that climate would produce less effect in the course of its ordinary oscillations than when it swings beyond the usual extremes. A change of climate can produce bare areas by direct action only when the change is sudden. A slow departure, even if permanent, would act upon existing vegetation only by modifying it through ecesis or adaptation. Indirectly, of course, climatic factors and processes may cause new areas through the cooperation of topographic or biotic agents.

Bare areas due to climatic factors directly.—The direct action of climatic factors takes place regularly through the destruction of existing vegetation. When the destruction is complete or nearly so, a bare area with more extreme water conditions is the result. The factors which act in this manner are: (1) drouth, (2) wind, (3) snow, (4) hail, (5) frost, and (6) lightning. In addition, evaporation, which is the essential process in drouth, produces new areas from water bodies in semiarid and arid regions. It may have the same effect on periodic ponds in humid regions. While the process is the same.

the degree to which it acts varies widely. Evaporation may merely reduce the water-level to a point where the ecesis of hydrophytes is possible, or it may continue to a point where islands, peninsulas, or wide strips of shore are laid bare to invasion. Finally, the lake or pond may disappear entirely, leaving a marsh, a moist or dry plain, or a salt crust.

Bare areas due to drouth.—The action of drouth in destroying vegetation and producing areas for colonization is largely confined to semiarid and arid regions. In humid regions it is neither frequent nor critical, while in desert regions it is the climax condition to which vegetation has adapted itself fully or nearly so. The usual effect is to produce a change in existing vegetation, but in regions like the Great Plains it sometimes destroys vegetation completely. As a rule, the destruction operates upon cultivated fields, simply freeing the area somewhat earlier for the usual development of a ruderal stage. It also occurs occasionally in tree plantations, with somewhat similar results. In native vegetation the complete destruction of a community is rare. When it does occur it is nearly always in lowland communities which have followed streams far beyond their climatic region. Ruderal and subruderal communities which pioneer in disturbed soils are the most frequent sufferers. In desert regions, which are characterized by communities of summer and winter annuals, the destruction of the latter by drouth before the vegetative season is over must occur occasionally. It has no significance for succession, however, as it is wholly periodic.

Bare areas due to wind.—The direct action of the wind upon vegetation is seen only in so-called "wind-throws" in forests. While areas in which trees have been blown down by the wind are frequent in some regions, they are local and of small extent. They are most apt to occur in pure stands of such trees as balsam, spruce, and lodgepole pine. "Wind-throws" are frequent in mountain regions where the soil is moist and shallow. The action of the wind affects only the tree layer, in addition to tearing up the soil as a consequence of uprooting the trees. It is supplemented by evaporation, which destroys the shade species by augmenting their transpiration greatly at a time when the holard is being constantly diminished by the drying out of the soil. As a consequence, "wind-throws" may become completely denuded of vegetation. In the case of completely closed forests, such as mature forests of the lodgepole pine (*Pinus murrayana*) and Engelmann spruce (*Picea engelmanni*), the fall of the trees amounts to denudation, since occasional saprophytes are often the only flowering plants left.

Bare areas due to snow, hail, and frost.—Bare areas due largely to snow are restricted to alpine and polar regions, where they occur usually in a zone between the area always covered with snow and that in which the snow disappears each summer. An abnormal fall or unusual drifting will cause the snow to remain in places regularly exposed each summer. After a winter of less precipitation or a summer of greater heat, the drifts or fields will melt, leaving a bare area for invasion. This frequently happens in the denser portions of coniferous forests, as well as in and around the outposts above the timberline. In such cases the resulting development has to do chiefly with the undergrowth.

The effect of frost in producing bare areas by destroying the plant population is almost negligible. Its action is confined almost wholly to cultivated

areas, such as orchards, fields, and gardens. In such places only the first pioneers of a ruderal population can appear, except in rare cases where the area is abandoned because of the frost. Communities of ruderal annuals are sometimes destroyed by frost, but this delays the usual course of succession for but a year at most. Native vegetation may be changed by the action of frost, but can rarely be wholly destroyed by it, because of the persistence of perennial species with underground parts. A single case of the destruction of native communities by frost was found in the dune areas of Medanos Spit, near San Diego, in southern California. The severe freeze of 1912 had completely killed many large families of *Mesembryanthemum*, and these still persisted as blackened areas in the spring of 1914. Such areas had been essentially denuded by frost, and were already being invaded by other pioneers.

The denuding action of hail is often very great. In some parts of the Great Plains destructive hailstorms are so frequent that they have caused the abandonment of farms and sometimes of whole districts. As with frost, the effect upon cultivated plants is very much greater than upon native vegetation. It is not infrequent to see the fields so razed by hail that not a single plant is left alive. Native communities often suffer great damage, especially broad-leaved forests and scrub, but the effect rarely approaches denudation. Grassland is sometimes mowed down also, but the effect is merely to favor the grasses at the expense of species with broad leaves or rigid stems.

Bare areas due to lightning.—The rôle of lightning in causing fire in vegetation has come to be recognized as very important (Bell, 1897; Clements, 1910; Graves, 1910; Harper, 1912). The majority of lightning strokes do not set fire to trees or other plants, and the attendant rain usually stops incipient burns. Even in such cases forest fires have actually been seen to start from lightning, and the number of such cases in the aggregate would apparently be large. In regions with frequent dry thunderstorms, *i. e.*, those unaccompanied by rain, such as occur especially in Montana and Idaho, lightning is the cause of numerous, often very destructive, fires. Once well started there is no difference in a forest fire due to lightning and one due to other agents, such as man, volcanic eruptions, etc.

Bare areas due indirectly to climatic factors.—These are due almost wholly to the effect of physiography in exceptional cases of rainfall, of run-off due to melting snow, or of wind-driven waters. In all three the process is essentially the same. The normal drainage of the area is overtaxed. The flood-waters reach higher levels than usual and are ponded back into depressions rarely reached. Moreover, they cover the lowlands for a much longer period. In the one case they form new water areas for invasion. Since these are usually shallow and subject to evaporation, the development in them is a short one. In the case of the lowlands, the vegetation of many areas is washed away, covered with silt, or killed by the water, and the area is bared for a new development. This is of course essentially what must have occurred at the end of each period of glaciation. The ponding back of glacial waters and the fluvio-glacial deposits were the outcome of the interaction of climate and physiography, just as can be seen in miniature at the foot of a glacier to-day.

Sudden changes of climate.—It is probable that there is no such thing as a sudden change of climate, apart from the striking deviations from the

normal that we are so familiar with. If the criteria of evolution and of historical geology are applied to climatology, it seems evident that even the climates of the past are largely to be explained in terms of present climatic processes (Huntington, 1914). If we consider the causes which are thought to produce the most striking and sudden deviations at present, namely, sun-spot maxima-minima and volcanic ash in the atmosphere, two facts are evident. The first is that the period between extremes is several years. Whatever the effect may be in sorting out the population, or in producing adaptation, it is clear that the intensities known, when spread over several years, are quite insufficient to destroy plant communities and thus denude habitats. The second fact is that there is no record of the destruction of vegetation at such periods, though doubtless the effects of frosts were then most marked. In consequence it seems impossible to regard changes of climate as initial causes of succession. They are effective only in modifying existing seres.

BIOTIC CAUSES.

General relations.—In considering the influence of animals and plants upon succession, it is necessary at the outset to distinguish clearly between biotic causes and biotic reactions. The former, like all initial causes, produce bare areas on which a new sere can develop. Biotic reactions, on the contrary, have nothing to do with the production of initial areas, but represent the modifying action of each stage upon the habitat. They are continuative, since they induce and control the successive waves of invasion which mark the various stages. A plant or animal parasite which produces a bare area by killing all the plants of a community, as may readily occur in families or pure stands of trees, is a biotic initial cause. Holophytes and saprophytes can only react upon the habitat by changing the factors of air or soil. Earthworms react upon the soil conditions, while rodents such as prairie-dogs both react and initiate new areas. It is the reactions of the plant communities upon the habitat which are of paramount importance. With the possible exception of *Sphagnum*, plants very rarely play the rôle of initial causes. The reverse is true of man and animals. They are initial causes of great frequence and wide-spread distribution, but only a few have a definite reaction upon the habitat.

Like climatic factors, biotic agents may change the existing vegetation, as well as initiate new vegetation. In both cases they have to do with development, but they can be regarded as causes of succession only when they produce bare areas in which invasion occurs. It is probable that animals change the course of development more often than they start it, while the activities of man lead largely to denudation.

Action and effect.—Man, and animals to a certain extent also, have at their command the initial processes already considered under topography. These are removal, deposit, draïnage, and flooding. In addition, they may destroy the vegetation, but affect the soil slightly or not at all. In the case of man, in particular, the most various activities result in similar processes and areas. It seems most natural to group them accordingly, rather than to consider them from the standpoint of the activities themselves. This is illustrated by the fact that fallow fields, roadsides, prairie-dog towns, and ant-hills in the prairie region exhibit essentially the same condition and initiate similar or identical developments. The most suggestive grouping in conse-

quence is the following: (1) activities that destroy vegetation without greatly disturbing the soil or changing the water-content; (2) activities which produce a dry or drier habitat, usually with much disturbance of the soil; (3) activities which produce a wet or wetter soil or a water area. There is clearly no sharp line of demarcation between the three groups, but this is evidence that the distinction is a natural and not an artificial one. The simplest and most convenient arrangement is one based upon agents and kinds of activity (Clements 1904:116; 1905:249; 1907:279), but this is not in fundamental relation to successional development.

Bare areas due to destruction of vegetation alone.—The primary activities by which man produces denuded areas are burns and clearings. Clearings result for the most part from lumbering or from cultivation, though a host of minor activities have the same result. Ant areas in arid regions are perhaps the best examples of clearing by animals without soil disturbance. In all cases of burning and clearing the intensity or thoroughness of the process determines whether the result will be a change of vegetation or the initiation of a sere. The latter occurs only when the destruction of the vegetation is complete, or so nearly complete that the pioneers dominate the area. Lumbering consequently does not initiate succession except when it is followed by fire or other process which removes the undergrowth. Most fires in woodland denude the burned area completely, but surface fires and top fires merely destroy a part of the population. Fires in grassland practically never produce bare areas for colonization. Poisonous gases from smelters, factories, etc., sometimes result in complete denudation, though the action is chiefly felt in a change of vegetation. Cultivation normally results in complete destruction of the original vegetation. In the broadest sense, a new sere starts with the sowing or planting of the crop. In the case of annual crops, however, real development begins only when cultivation is abandoned. In new or sparsely settled grassland regions, the wearing of roads or trails results in a characteristic denudation with little or no soil disturbance. Complete denudation by animals is only of the rarest occurrence, except where they are restricted to limited areas by man. Even in striking cases of the destruction of a forest by parasites, such as the repeated defoliation of aspens by caterpillars, the undergrowth is little affected. Complete destruction by parasites usually occurs only in the case of annual crops. A striking example of denudation by a plant parasite was found on the shores of False Bay in southern California, and especially on the dunes of Medanos Spit. Here families and colonies of *Abronia umbellata* and *Franseria bipinnatifida* were completely covered with an orange mat of *Cuscuta salina.* The dodder in May had already killed many of the families entirely, and it was obvious that many more would suffer the same fate. With the gradual death of the hosts, the dodder became brown and dried up with the host plants. The two were then gradually blown away by the constant onshore winds and a bare sand area was left.

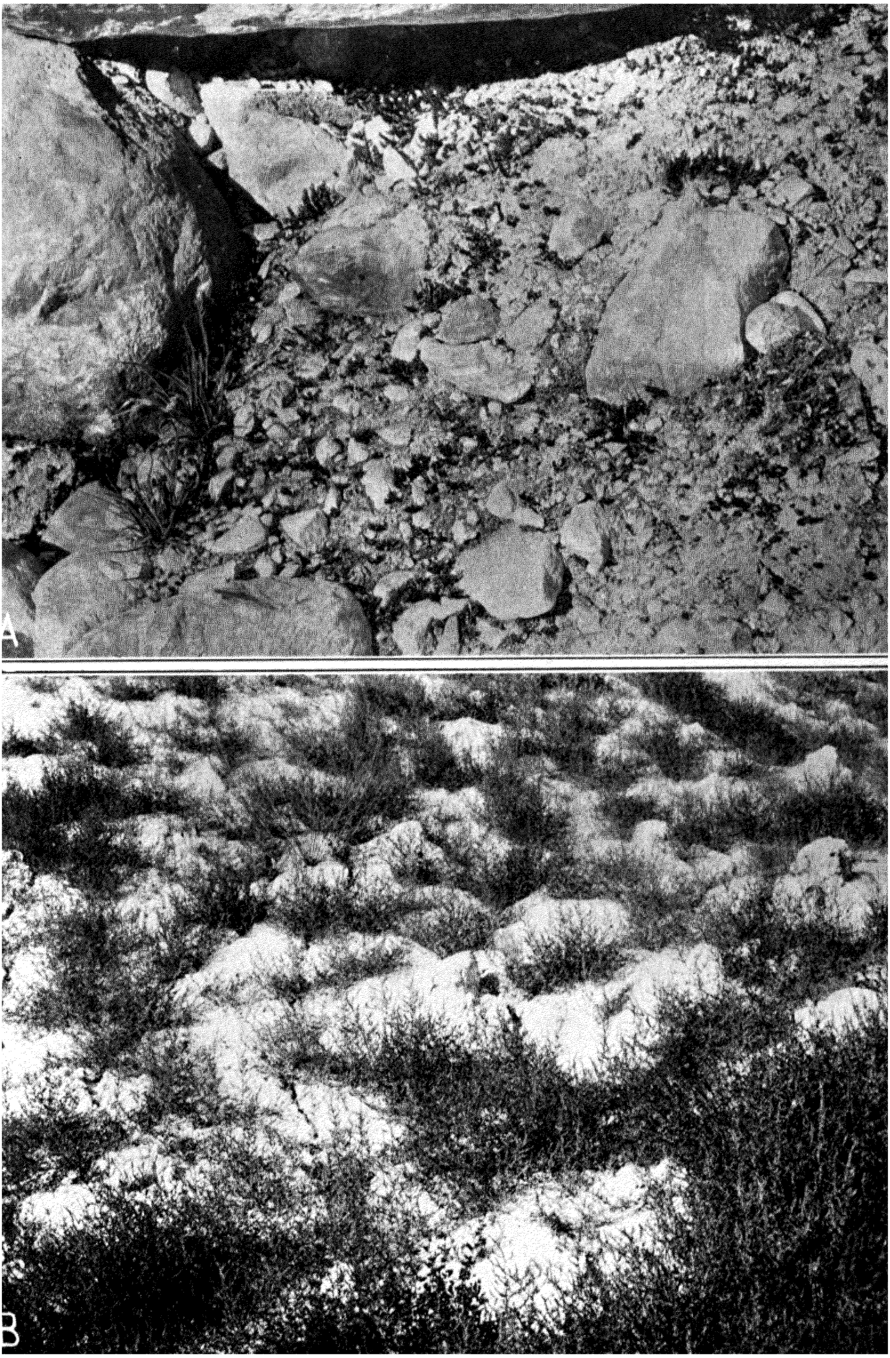
Bare areas with dry or drier soils.—These occur chiefly where there is a marked disturbance of the soil. The latter affects the water-content by changing the texture, by changing the kind of soil, as from clay to sand or gravel, or by both methods. These results may be produced by removal, by deposit, or by the stirring of the soil in place. In the case of man they are produced

by the widest variety of construction and engineering processes, with roads and railroads as universal examples. The removal and deposit of soil by animals is confined to the immediate neighborhood of the burrows of rodents, the homes of ants, etc. In some cases, such as densely populated prairie-dog towns, the burrows are sufficiently close to produce an almost completely denuded area. Insignificant as most areas of this sort are, they give rise to real though minute seres of much value in communities otherwise little disturbed.

Bare areas with wet soils or water.—As indicated under topographic causes, draining and flooding may bring two different areas to the same condition for invasion. The habitats produced by both are similar in having a wet soil, capable of colonization only by hydrophytes or marsh-plants, except in cases where drainage is reinforced by rapid or excessive evaporation. This is true of the canals and ditches, as well as of the areas actually drained or flooded, and equally so of all canals and ditches, regardless of their purpose. Again, it is unimportant whether flooding, for example, is brought about by the diversion of a stream of water or by the construction of a dam. It is equally immaterial whether the dam is built by man or by beavers. The essential fact is that the water-content will be excessive and that the pioneer stages will consist of hydrophytes in all these cases. The effect of drainage, *i. e.*, relative lowering of the water-level, can be produced by filling, just as flooding can be caused by the formation of a depression due to the removal of soil. An exceptional instance of the former is furnished by the case of coral reefs and islands.

PRIMARY AND SECONDARY AREAS.

Distinction.—The whole course of succession rests upon the nature of the bare area which initiates it. We have already seen that the essential nature of a bare area is expressed in the amount and kind of water. Hence, in attempting to group naturally all the foregoing areas, *i. e.*, from the standpoint of succession, it is necessary to recognize that water areas and rock areas constitute the two primary groups. While these are opposed in water-content and density, they agree in presenting extreme conditions in which development is necessarily slow and of long duration. The denudation of either area in the course of succession results in the sudden reappearance of earlier conditions, which cause the repetition of certain stages. If denudation consists in the destruction of the vegetation alone, the soil factors are changed relatively little. The sere thus initiated is relatively short, consisting of fewer stages and reaching the climax in a short time. If the soil is much disturbed, however, the conditions produced approach much nearer the original extreme, and the resulting sere is correspondingly longer and more complex. The degree of disturbance may be so great as to bring back the original extreme conditions, in which case the normal course of development is repeated. This amounts to the production of a new area, both with respect to the extreme condition and the lack of germules. Hence, all bare areas fall into a second basic grouping into primary and secondary areas. Primary bare areas present extreme conditions as to water-content, possess no viable germules of other than pioneer species, require long-continued reaction before they are ready for climax stages, and hence give rise to long and complex seres. Sec-



A. Primary area colonized by mosses, terminal moraine of the Illecillewaet Glacier, Glacier, British Columbia.

B. Secondary area colonized by *Salsola*, on a railway embankment, bad lands, Scott's Bluff, Nebraska.

ondary bare areas present less extreme conditions, normally possess viable germules of more than one stage, often in large number, retain more or less of the preceding reactions, and consequently give rise to relatively short and simple seres. From the standpoint of succession, secondary areas are related to primary ones. In consequence, the most natural classification of all bare areas seems to be into primary and secondary, with a subdivision into water, rock, and soil (plate 6, A, B).

Sterility of primary and secondary areas.—As stated above, primary areas, such as lakes, rocks, lava-flows, dunes, etc., contain no germules at the outset, or no viable ones other than those of pioneers. Secondary areas, on the contrary, such as burns, fallow fields, drained areas, etc., contain a large number of germules, often representing several successive stages. In some cases it seems that the seeds and fruits for the dominants of all stages, including the climax, are present at the time of initiation. The sterility of the soil of a primary area is due chiefly to the relatively long period of its formation, and to the effect of excessive water-content or drouth upon migrating germules. In all cases it arises in a measure also from the impossible conditions for the ecesis of all plants except pioneers. In these points most secondary soils offer a sharp contrast. The method of origin permits the persistence of seeds or perennial parts or both, and its suddenness usually allows the immediate entrance of many migrants. The soil affords favorable conditions for the preservation of seeds and fruits, often for many years, as of course for ready ecesis (plate 9, A, B).

This contrast between primary and secondary areas is seen most strikingly in the case of land-slips, where the slip exposes rock on the mountain side and produces a mass of soil and vegetation at the bottom. This is sometimes true also of the fragmentation of cliffs by gravity and of erosion and deposit due to torrential rains or other agents which act suddenly.

Denudation.—Secondary areas are the result of denudation, with or without the disturbance of the soil. Their nature is dependent upon the process of denudation and upon the degree to which it acts. The latter is ordinarily much the more important. It determines in the first pdace whether the result will be merely a change in the existing community or the production of a bare area. In the case of the complete removal of vegetation, as by fire, the soil may be disturbed so little that it offers essentially the same conditions as before denudation, and initiates a sere correspondingly brief and simple. On the other hand, the disturbance of the soil may operate to various depths and produce correspondingly extreme conditions up to the final extremes, water and rock, which constitute new areas. The production of new areas by denudation and soil disturbance is relatively infrequent, however.

Methods of denudation.—Denuding forces operate normally by the destruction of vegetation, accompanied by the disturbance or removal of the soil. Destruction may, however, be a consequence of flooding or deposit. Apart from the destruction of the existing population, it is the depth of removal or deposit of soil which is critical. The rate of removal or deposit often plays an important part also, though it is usually expressed in depth. In burns there is practically no disturbance of the soil at all, though its composition may be materially affected. Cultivation disturbs soil, changing its texture and water-content in different degrees. Construction and engineering

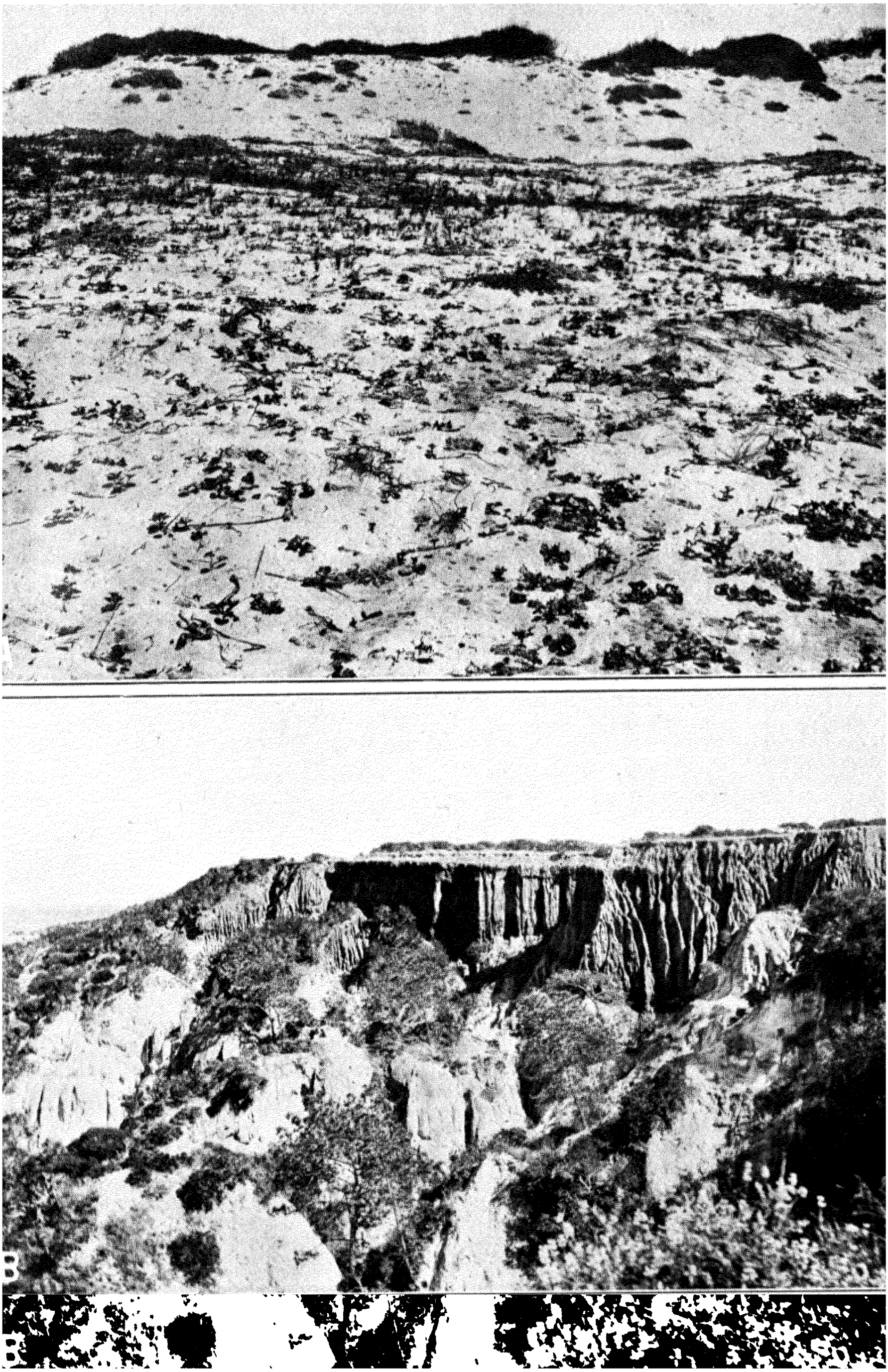
operations effect removal and deposition of the soil in varying degree. Because of its action in destroying vegetation, water must be considered in this connection also, especially in the case of flooding. Climatic initial causes produce denudation alone, while topographic ones exhibit the same wide range of effect shown by biotic causes.

Depth of removal or deposit.—The reaction of plants upon the soil is confined wholly or chiefly to the layer in which the roots grow. This depth establishes the limit to which removal may ordinarily go without changing soil conditions essentially. In the early stages of very loose soils, such as the sand of bars and dunes, the reaction is slight, but it seems probable, however, that these, too, must follow the general rule, namely, that the removal of the soil built up by reaction must necessitate a return to primary conditions. In the vast majority of cases a secondary area is formed whenever removal operates within the root layer of soil. This may be readily tested by instrumental methods or by experiment. In general, the composition of the initial stage of the sere indicates this clearly enough. The removal of this layer to different depths is reflected in the composition and length of the resulting secondary sere or subsere.

In cases where the destruction of the vegetation is accompanied or followed by the deposition of soil, the nature of the bare area will be decided by the kind of soil deposited as well as by its depth. If sand or gravel are laid down over loam to a sufficient depth, the water relations of the area may be moved to one extreme and a primary habitat result. Here the depth must approximate the length of the root system of the species of the initial stages. Otherwise the roots will reach the original soil and the development will be controlled in some degree by the latter. When the depth of added soil exceeds 1 or 2 meters, a secondary succession can result only when the soil is essentially similar in texture and water relations to the original. This is apparently true in the majority of cases (plate 7, A, B).

The effects of the removal of water by drainage or of the addition of water by flooding may be alike or unlike. Either flooding or drainage may destroy a plant population and yet leave the area little changed, thus initiating a secondary succession. This is the regular effect of drainage when it does not merely modify the existing vegetation. In the case of ponding, however, the water produces a new set of extreme conditions, and this constitutes a primary area.

Rate and extent of removal.—Destruction of a community with accompanying or subsequent removal of the soil is the general process of which topographic erosion is much the most important part. In fact, erosion may well be regarded as the general process, which is produced by topographic, climatic, or biotic forces. While depth is the final criterion of the effect of erosion, both its rate and extent have an influence. Erosion to a depth of a foot would produce different conditions when caused by a single torrential rain from those due to gradual erosion spread over several years, though in both cases the resulting area would normally be a secondary one. The differences would consist as much in the stability of the surface for migration and ecesis as in the water relation. The extent of the denuded area is closely related to depth of erosion. When the latter is local, it is less apt to depart widely from the normal condition, and its invasion is controlled almost completely by the parent area. This matter is discussed in detail in the section on cycles of erosion.



A. Superficial wind erosion, Dune Point, La Jolla, California.
B. Deep-seated water erosion, Torrey Pines, Del Mar, California.

IV. ECESIC CAUSES.

Nature.—As has been indicated, succession owes its distinctive character to the communities which succeed each other in the same area. This character is given it by the responses or adjustments which the community makes to its habitat, namely, migration, ecesis, competition, and reaction. These are the real causes of development, for which a bare area does little more than furnish a field of action. To them is due the rhythm of succession as expressed in the rise and fall of successive populations. They may well be regarded as the paramount causes of succession, since their action and interaction are the development of vegetation. As every sere must begin with a denuded area and end in a climax, it is clearer to treat them along with initial causes and climax causes.

AGGREGATION.

Concept and rôle.—Aggregation is the process by which germules come to be grouped together (Clements, 1905:203; 1907:237). It consists really of two processes, simple aggregation and migration. These may act alone or together, but the analysis is clearer if each is considered separately. By simple aggregation is understood the grouping of germules about the parent plant. Even in the fall of seeds there is often some movement away from the parent plant, but it can not properly be regarded as migration, unless the seed is carried into a different family or into a different portion of the same colony or clan. The distinction is by no means a sharp one, but it rests upon two factors of much importance in vegetation. The first is that movement within the parent area bears a different relation to ecesis from movement beyond the parent area. The second fact is that simple aggregation increases the individuals of a species and tends to produce dominance, while migration has the opposite effect (plate 8 A).

Simple aggregation may operate by seeds and fruits, by propagules, or by both. The method of aggregation plays an important part in determining the germules in secondary areas, and in the initial stages of a sere. In this respect it is essentially like migration, and will be considered in connection with the discussion of the parts used as migrules.

Effects of simple aggregation.—Aggregation usually modifies the composition and structure of existing communities. This effect is seen most strikingly where the vegetation is open, though it is readily disclosed by the quadrat in closed communities. The increase of population in the case of the pioneers of a bare area is mainly a matter of aggregation. Conspicuous examples of this are found in areas with unstable soil, such as gravel-slides, blow-outs, bad lands, etc. The influence of aggregation is especially important in communities which are destroyed by fire, cultivation, etc. In many instances the change in soil conditions is slight, and the course of succession is determined by the number of germules which survive. If the number is large, as in certain forest areas, the resulting sere is very short, consisting only of the stages that can develop while the trees are growing to the size which makes them dominant. When the number of aggregated germules is small or none, the selective action of migration comes into play, and the course of development is correspondingly long.

Relation to denuded areas.—Aggregation is the normal result of seed-production in a community. Its importance in secondary areas depends wholly upon whether it occurs before or after the action of the denuding agent. Normally, of course, it occurs before denudation, and the question is chiefly one of the kind and number of germules which escape destruction. This is determined by the agent, the position of the germule, and sometimes by its nature. In the case of fire, seeds and fruits on the surface or near it are destroyed, unless they have unusual protection, as in some woody cones. Fruits buried by rodents, or seeds and fruits which become covered with moist duff, often survive. In cultivated areas, seeds often persist for a long time, though they play no part in succession unless they survive until the field is abandoned. On the other hand, intensive cultivation destroys all underground parts, while fire has little or no effect upon them. In grassland the effect is merely to modify the population, but in woodland succession results.

Aggregation occurs after fire only in a few striking instances. It occurs in the case of many conifers with large or hard cones, especially where the fire kills the trees but leaves them standing. This is often true of lodgepole pine (*Pinus murrayana*), jack pine (*P. divaricata*), and all others in which the cones remain closed and attached to the branches for a long time.

Interaction of aggregation and migration.—All sterile bare areas owe their pioneers to migration. After the establishment of the first invaders the development of families and colonies is due primarily to aggregation (plate 8 B). The appearance of each successive stage is caused by the interaction of the two processes. Migration brings in the species of the next stage, and aggregation causes them to become characteristic or dominant. Their relation in each stage is shown in the development of the succession as a whole. Migration marks the beginning of the sere, as of each stage. It becomes relatively more marked for a number of stages, and then falls off to a minimum. In dense closed forests it becomes extremely rare, and the ecesis of the migrants impossible. On the other hand, aggregation becomes more marked with successive stages, and a sere may end in what is essentially a family, *e. g.*, a pure stand of *Pseudotsuga* or *Picea* with practically no undergrowth.

MIGRATION.

Concept.—The nature of migration as an essential process in succession has been analyzed in detail elsewhere (Clements, 1904:32; 1905:210; 1907:240). It will suffice to summarize the main points in connection with indicating their special bearing upon the nature and course of succession. The use of the term is restricted to its proper sense of movement. Migration is regarded as a process distinct from establishment or ecesis. The two are most intimately related in the general process of invasion, which comprises movement into a habitat and establishment there. Migration begins when a germule leaves the parent area and ends when it reaches its final resting-place. It may consist of a single movement, or the number of movements between the two places may be many, as in the repeated flights of pappose and winged fruits. The entrance of a species into a new area or region will often result from repeated invasions, each consisting of a single period of migration and ecesis.

Mobility.—Mobility is the ability of a species to move out of the parent area. Among terrestrial plants, it is indicated chiefly by the size, weight, and

surface of the disseminule. This is particularly true of seeds and fruits carried by wind and water. Man and animals distribute fruits for so many reasons and in so many ways that the only test of mobility in many cases is the actual movement. This is especially clear in the case of many weeds of cultivated fields, which owe their migration wholly to their association. Mobility is also directly affected by the amount of seed produced. It is increased by large seed-production, both on account of the large number of seeds or fruits and the correspondingly smaller size.

The relation of mobility to succession is obvious. In bare land areas, and especially in denuded ones, the order of appearance of species is largely a matter of the size and modification of the disseminule. The earliest pioneers—lichens, liverworts, and mosses—usually have microscopic germules, whether spores, soredia, or gemmæ. The early herbaceous pioneers are grasses and herbs with small seeds and fruits, well adapted for wind-carriage, as in fire-grass (*Agrostis hiemalis*) and fire-weed (*Chamaenerium angustifolium*), or mobile by virtue of association, as in *Brassica, Lepidium, Chenopodium,* etc. The sequence of shrubby species is determined partly by mobility, as is true of *Rubus* in burns, *Salix* in lowlands, and *Cercocarpus* in grassland. The same relation is shown in trees by the fact that *Populus* and *Betula* are everywhere woodland pioneers. Trees constitute the climax life-form, however, and their successional relation is chiefly due to other factors.

Seed-production.—The absolute seed-production of a species bears a general relation to its power of invasion. The latter is expressed more exactly by the efficient seed-production, which is the total number of fertile seeds left after the usual action of destructive agents. The number of seeds produced by a tree of *Pinus flexilis* is large, but the efficiency is almost *nil*. The toll taken by nut-crackers, jays, and squirrels is so complete that no viable seed has yet been found in hundreds of mature cones examined. The fertility of seeds is greatest in typical polyanthous species which produce but one seed per flower, such as grasses, composites, and other achene-bearing families. This is shown by the large number of successful invaders, *i. e.*, weeds, produced by these groups. Fertility is often low in polyspermous plants, due to the lack of fertilization or to competition between the ovules. The number of seeds is often correlated with size, but the exceptions are too numerous to permit the recognition of a general rule. The periodic variation in the total seed-production is a factor of much importance, especially in trees and shrubs. This is due to the fact that birds and rodents consume practically the entire crop in the case of conifers, oaks, etc., during poor seed-years. The efficient production is high only during good years, and the invasion of such species is largely dependent upon the occurrence of good seed-years.

The influence of seed-production is felt in mobility, in ecesis, and in dominance. Its effect can only be estimated at the present, owing to the lack of exact study. It is probable that the quantitative investigation of the seed-production of dominant and characteristic species will go far towards revealing the real nature of dominance.

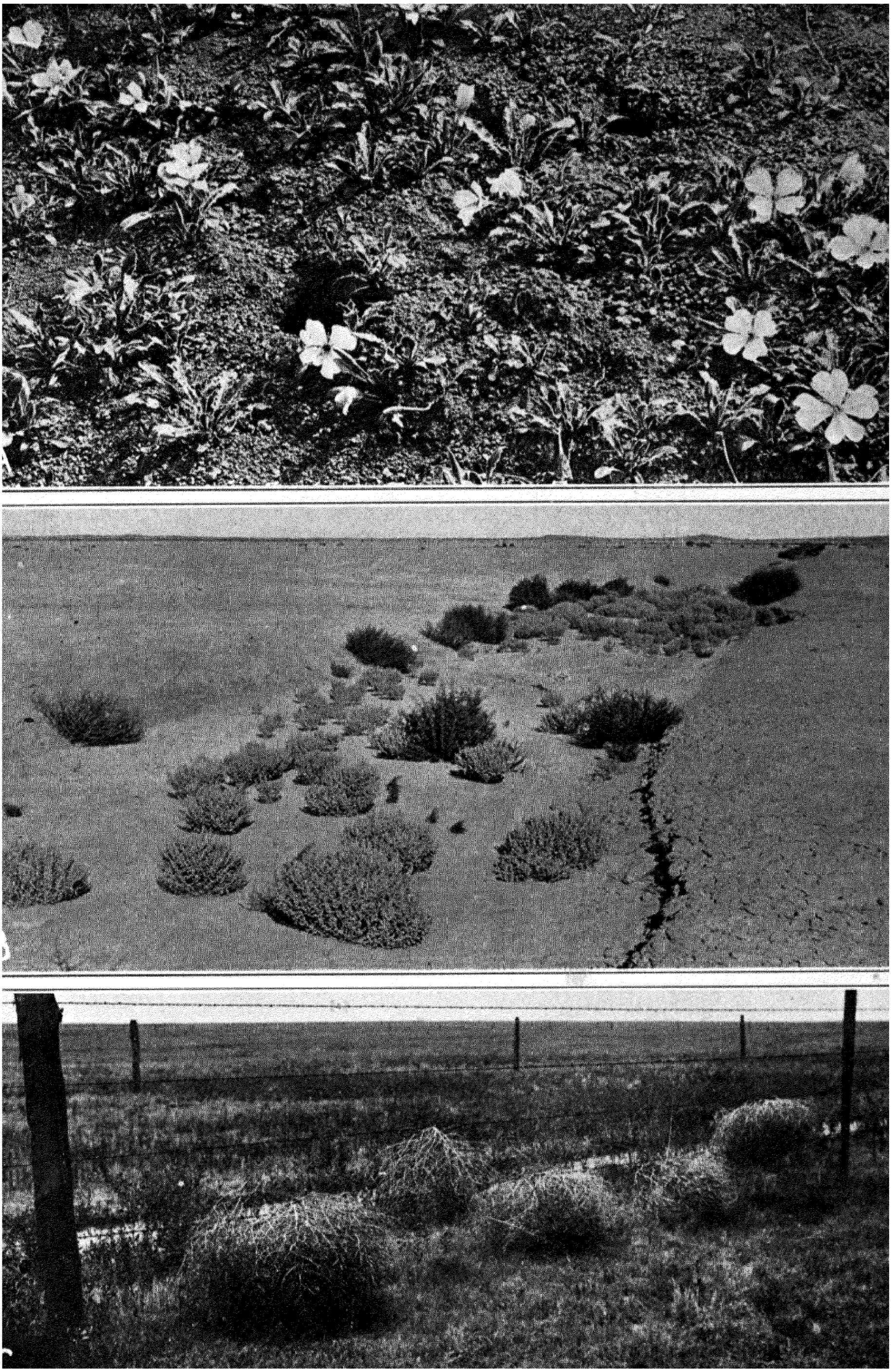
Influence of the organ used.—When runners, stolons, and rhizomes carry buds several to many feet from the parent plant, the result may well be regarded as migration rather than aggregation. Such migration plays a small part in the colonization of new areas. It is almost negligible in comparison

with the migration of free parts, such as spores, seeds, and fruits, especially in large areas. Naturally, species which are readily carried by seeds and fruits, and move also by offshoots, form excellent pioneers. The influence of size of organ is indicated by the relative mobility of spores, seeds, and fruits. In spite of many exceptions, spores are more readily and widely distributed than seeds, and seeds than fruits. This is shown in some measure also by the success in migration of plants in which the fruit simulates a seed almost perfectly, as in the grain, achene, etc. The handicap of the fruit in regard to size is often counterbalanced by the perfection of the contrivance for dissemination. In the case of tumbleweeds and tumbling grasses, the whole plant or the major portion of it has assumed a form which amounts practically to a nearly perfect contrivance for effective migration (plate 8 c).

Influence of the migration contrivance.—The effect of the modification for carriage is intimately blended with that of the agent, as would be expected. The perfection of the device determines the success of the agent, as is well seen in those modifications which increase the surface for wind carriage. Sack and bladder fruits, as in *Physalis,* are relatively ineffective, and are often associated with other devices. Wings give greater buoyancy, but are only moderately efficient, except when the seed or fruit is small and light. The vast majority of samaras of the elm, maple, ash, etc., fall near the parent tree. This is strikingly true of the seeds of conifers. A careful transect study of the flight of seeds of the spruce and the fir showed that practically all of them landed within a distance equal to the height of the tree. Comate and pappose seeds and fruits are by far the most efficient of wind-borne disseminules, and probably of all kinds as well. Here again success is determined largely by smallness of size, but apart from this the perfection of the device as to the number, length, and position of scales or hairs is decisive. Scales are less efficient than bristles or hairs, and the latter are successful in proportion to length and number. Disseminules tufted at one end are carried more readily than those covered with hairs, and a pappus which spreads widely or is plumy is the most effective of all. The relative efficiency of devices for carriage by animals is less evident, but the number of pioneers which possess fruits with spines or hooks is significant.

Many fruits migrate readily, even when the migration device is not greatly perfected. This is due to the fact that they avail themselves of two or more agents, either by means of two distinct devices or because of their behavior on drying. In *Physalis* the bladdery fruit is rolled over the ground by the wind, and then the seeds scattered by birds and rodents. *Stipa, Erodium,* and other plants with sharp-pointed twisting fruits, are carried by attachment and blown by the wind in tangled clusters, the two agents often alternating many times. A striking case of this sort is afforded by *Micrampelis,* which is a frequent pioneer in denuded areas along streams. The fruits are blown by the wind, floated by streams, and even carried by attachment, while the seeds, in addition to being forcibly expelled, are readily carried by water.

The distance of migration is a direct consequence of the perfection of the device. Hence the latter is of the first importance in selecting the migrants which are moving toward a new area. It thus plays a large part in determining what species will enter it as pioneers, as well as the stages in which others will appear. The comate seeds of fireweed, aspen, and willow may be carried for



A. Family of *Pachylophus caespitosus* on gravel-slide, Alpine Laboratory, Colorado.
B. Colony of *Suaeda* and *Atriplex* in a depression, bed of a former salt lake, Hazen, Nev.
C. Tumbleweed, *Salsola*, on the Great Plains, Akron, Colorado.

at least several miles in such quantities as to produce dominance. Dominance in the development in secondary areas, especially, is directly dependent upon the number of seeds which enter, and hence upon the migration device. If seeds or one-seeded fruits migrate singly, the resulting individuals stand separated, and dominance results only from the movement of large numbers. In a relatively large number of cases, several-seeded or even many-seeded fruits migrate, and upon germination produce the nucleus of a community. Often, also, fruits become tangled with each other, as in *Stipa, Erodium, Xanthium, Desmodium,* etc., and are transported to new areas, when they produce families. This is particularly true of tumble-weeds (*Salsola, Cycloloma, Amaranthus,* etc.), and of tumble-grasses (*Panicum capillare, Eragrostis pectinacea,* etc.).

Rôle of migration agents.—It is significant that the agents which carry migrules, viz, wind, water, gravity, glaciers, man, and animals, are also the initial causes of bare areas. Thus, the force which produces an area for succession also brings the new population to it. Often the two processes are simultaneous, especially in denuded habitats. The relation is as simple as it is intimate. Water as a migration agent brings to new water or soil areas chiefly those germules which can be gathered along its course. Thus it is self-evident that a new area with an excess of water will be provided for the most part with water-borne migrules, and that the viable ones will practically all be of this kind. The action of wind is broader, but it is clear that initial areas due to wind are found only in wind-swept places, which are of course where the wind will carry the largest load of migrules. An extremely close connection is found also in the talus slopes due to gravity, for the majority of the species are derived from above. The universal prevalence of ruderal plants in denuded areas due to man's activities is sufficient evidence of the direct relation here.

Destructive action of agents.—The action of water upon seeds practically eliminates all but hydrophytic or ruderal species as pioneers in water or wet areas (Shull, 1914:333), though this effect is doubly insured by the difficulties of ecesis. Large quantities of seeds are also destroyed in all areas produced by deposit, and especially in talus. The action of seed-eating agents, particularly birds and rodents, is often completely decisive. This is seen most strikingly in secondary areas, but it occurs in all places where seeds are exposed. So complete is the destruction of seeds in certain instances, notably in forests of lodgepole pine, that the reappearance of certain species is possible only where the rodent population is driven out or destroyed. This is confirmed by the almost uniform failure of broadcast sowing in reforestation, as well as in other methods of sowing when the birds and rodents are not destroyed. No other factor in invasion has been so often overlooked, and its exact value is consequently hard to determine. If the few quantitative results so far obtained are representative, it must be regarded as of great and often of critical importance.

Direction of migration.—While migration tends to radiate in all directions from the parent group, it often comes to be more or less determinate. In general, it is radial or indeterminate when it is local, and unilateral or determinate when more general. The local movement due to wind, man, or animals may be in any and all directions, while distant migration by either agent will usually be in one direction. This is peculiarly true of carriage by streams, in which the regular movement is always down the valley. In the floristic

study of vegetation, distant migration has appeared more striking and interesting than local. It is in no degree as important in the study of succession, as local migration is primarily responsible for the population of new areas. Here, again, exact observations and experiments are few, but most of the evidence available shows that effective invasion in quantity is always local. This is doubtless true of great migrations such as those of the glacial and post-glacial times, when population moved hundreds of miles. These were apparently only the gross result of repeated local movements, acting in the same general direction through long periods.

Up to the present time the study of succession has been almost wholly confined to examining and correlating communities during one or a few seasons. The development has not been followed in the various portions of its course, but has been reconstructed from the end results, *i. e.*, the communities. While the whole course of a primary sere can be obtained in no other way, every one of its stages permits quantitative study of its own development. Secondary seres may often be studied as processes in their entirety, owing to their much shorter course. In such work the position of the bare area with reference to the migration agents active is of the first consequence. An area surrounded by a community of the successional series will be quickly colonized by immigration from all sides. One lying in the ecotone between two associations will have its development influenced by the prevailing direction of movement. This is well illustrated by the behavior of new areas just below timber-line on mountains. The area belongs to the forest climax, but it is invaded and held by alpine species for a very long time, if not permanently. This is due to the ease with which seeds and fruits from the alpine area above are brought to the area by gravity, and to the extreme difficulty the forest migrules find in moving up the slope. Man and animals are the only agents which can overcome this effect. The only exception is furnished by small comose seeds, such as those of the fireweed and aspen, which may be carried hundreds of feet up mountain sides by the wind.

ECESIS.

Nature and rôle.—Ecesis is the adjustment of the plant to a new home (Clements, 1904:50; 1905:220; 1907:261). It consists of three essential processes, germination, growth, and reproduction. It is the normal consequence of migration, and it results sooner or later in competition. Ecesis comprises all the processes exhibited by an invading germule from the time it enters a new area until it is thoroughly established there. Hence it really includes competition, except in the case of pioneers in bare areas. The ecesis of a social plant is the same as that of an isolated invader in essentials, but it takes place under conditions modified by the neighboring plants. Hence it promises clearer analysis if ecesis is considered first and competition subsequently.

Ecesis is the decisive factor in invasion. Migration is wholly ineffective without it, and at present, indeed, is usually measured by it. The relation between the two is most intimate. Ecesis in bare areas especially depends in a large measure upon the time, direction, rapidity, distance, and amount of migration. There is usually an essential alternation between the two, since migration is followed by ecesis, and the latter then establishes a new group

from which further migration is possible, and so on. The time of year in which fruits ripen and migration occurs has a marked influence upon the establishment of a species. Migrules ordinarily pass through a resting-period, but are frequently brought into conditions where they germinate at once and then perish, because of unfavorable conditions, or because of competition. The direction and distance of movement are decisive in so far as they determine the kind of habitat into which the seed is carried. The number of migrants is likewise important, since it affects the chances that seeds will be carried into bare areas where ecesis is possible.

In the case of algæ, migration and ecesis become nearly or quite synonymous, since plants of this sort are at home almost anywhere in the water. Indeed, it may be said that they are always at home, because they remain in the same habitat, no matter where carried. With aquatic flowering plants the case is somewhat different. The plants when free behave much as algæ do in regard to ecesis, but each new individual has to go through the processes of germination and growth. This is similar to what occurs in the aggregation of land plants. The seeds or underground buds do not find themselves in a new home exactly, but, apart from the greater certainty of success, the course of ecesis is the same.

The term *ecesis*, from the Greek *οἴκησις*, the act of coming to be at home; hence, adjustment to the habitat, or *οἶκος*, was first proposed (Clements, 1904:32) to designate the whole process covered more or less completely by acclimatization, naturalization, accommodation, etc. It has proved so definite and convenient in use that it seems desirable to employ a corresponding verb, *ecize* from *οἰκίζω*, to make a home, colonize.

Germination.—The first critical process in ecesis is germination. The exact scope of germination is debatable, but in nature it is most convenient to regard it as including the appearance and unfolding of the first leaf or leaves, whether cotyledons or not. It occurs regularly when a viable seed meets favorable conditions as to water, heat, and oxygen. It is often delayed or even absent when the seeds of native species are first sown under cultivation, and it is probable that germination is often delayed in nature, even when conditions seem favorable. A viable seed must contain a normal embryo, capable of absorbing water, and using the stored food for growth and consequent escape from the seed-coats. The amount of water, heat, and oxygen present must suffice to bring the seedling to the point where it can make food and begin its own independent existence. Hysterophytes are naturally exceptions.

With the exception of seeds of forest trees and certain ruderals, we have practically no accurate knowledge of the germinability of native species, especially at those times when conditions favor germination. The normal period of viability under the usual conditions of natural sowing is also unknown, as well as viability under extremely favorable and unfavorable conditions. In most cases the period of duration is a function of the seed-coats or pericarp, but in some viability is inherent in the embryo itself. The control of the habitat is two-fold. It determines whether the seed will germinate either immediately or during the season. If germination is delayed, it determines whether conditions will permit the seed to remain dormant but viable for several years. Habitats which are most favorable to germination are least favorable to dormant seeds, and, conversely, those which allow seeds to persist

for long periods are inimical to germination. In many cases, of course, the surface layer favors germination, and deeper layers, persistence.

Successful germination usually occurs only at proper depths, with the exception of bare areas with wet or moist surfaces. A few species have the peculiar property of being able to plant themselves when they germinate on the surface, but the rule is that seeds must be covered with soil to permit ecesis. This is particularly true of seeds on a forest-floor covered with a thick layer of leaves or needles, which prevent the root from striking into the soil. There is doubtless an optimum depth for each species, which varies more or less with the habitat. Too great a depth prevents the seedling from appearing altogether, or causes it to appear in such abnormal condition that it quickly succumbs. In the former case it may lead to dormancy, and germination after the area has been cleared or burned. The effect of depth and its relation to size of seed has been shown by Hofmann (1916) in the case of conifers. In *Pinus ponderosa,* with the largest seeds, 96 per cent germinated and 86 per cent appeared above ground at a depth of 1 inch, while only 36 per cent germinated and none appeared at 4 inches deep. In the case of *Pseudotsuga,* 93 per cent germinated and appeared at 0.5 inch, but only 17 per cent germinated at 4 inches and none appeared. For *Tsuga heterophylla,* at 0.25 inch the percentage was 96 and at 1.25 inches 42 per cent and 0, and for *Thuja plicata,* with the smallest seeds, 78 per cent at 0.12 inch and 26 per cent and 0 at 1 inch. The same investigator found that seeds of *Pinus monticola, Pseudotsuga,* and *Tsuga heterophylla* remained dormant in the soil for 6 years, those of *Taxus brevifolia* for 8, *Abies amabilis* for 5, *A. nobilis* for 3, and *Thuja plicata* for 2 years. While this is a relatively short time in comparison with the period in some ruderal species, it is of much more significance in succession.

Fate of seedling.—The crucial point in ecesis is reached when the seedling is completely freed from the seed-coat and is thrown upon its own resources for food and protection. Even before this time, invading seedlings are often destroyed in great numbers by birds and rodents, which pull them up for the food supply still left in the seed-coats. The tender seedlings are often eaten by the smaller chipmunks, and sometimes coniferous seedlings seem to be pulled up or bitten off in mere wantonness. In regions where grazing occurs, the destructive action of the animals is very great, especially in the case of sheep. Some toll is taken by damping-off fungi, such as *Pythium* and *Fusarium,* in moist, shady soils, but these are perhaps never decisive, except in artificial conditions. In the case of herbs, the greatest danger arises from excessive competition, especially in the dense aggregation typical of annuals. The direct effect is probably due to lack of water, though solutes and light may often play a part. With the seedlings of woody plants the cause of the greatest destruction is drouth in midsummer or later. This is the primary factor in limiting the ecesis of many conifers, though the "heaving" action of frost is frequently great or even predominant. The root-system is often inadequate to supply the water necessary to offset the high transpiration caused by conditions at the surface of the soil. Moreover, it is likewise too short to escape the progressive drying-out of the soil itself. In open places in the Rocky Mountains, such as parks, clearings, etc., the late summer mortality is excessive, often including all seedlings of the year. On the forest-

floor itself it is considerable or even decisive in places where a thick layer of dry mold or dust increases the distance roots have to go. Shreve (1909:289) has found that the seedling mortality of *Parkinsonia* in the deserts of Arizona was 70 per cent during the first year and 97 per cent by the end of the third year.

Growth.—If the seedling establishes itself, it is fairly sure to develop. This seems to be the rule with herbaceous plants, though it suffers some exceptions in the case of trees and shrubs. Even though conditions become more extreme, the old plant is usually better able to resist them. With increasing size of individuals the demands increase correspondingly. Hence, growth causes an increasing competition. Out of this competition some species emerge as dominants, reacting upon the habitat in a controlling way and determining the conditions for all other species in the community. Others represent an adaptation to conditions caused by the dominance and play always a subordinate part. A third behavior is shown by those species or individuals ordinarily capable of becoming dominant, whenever they appear tardily, or reproduce under unfavorable light intensities. The growth is diminished and the plant becomes suppressed. In forest and thicket suppression is progressive, and usually results in death, either through insufficient nutrition or in consequence of the attacks of insects and fungi. While suppression occurs in all degrees, its most important effect lies in inhibiting reproduction, and it would be well if the term were restricted to this sense.

Reproduction.—The invasion of a bare area is made possible by reproduction or seed-production in the neighboring communities. The development of each stage in the resulting sere is the consequence of the excess of reproduction over immigration. Reproduction is in consequence the final measure of the success of ecesis. In terms of succession at least, ecesis occurs only when a species reproduces itself, and thus maintains its position throughout the stage to which it belongs. In changes of vegetation the total period of ecesis may be much shorter; in fact, annuals may appear and disappear finally in a single season. In the case of annuals it is evident that there is no ecesis without reproduction. With perennials it is less clear, but there are few species that can maintain themselves in an area by vegetative propagation alone. Since bare areas are rarely invaded in this way, complete ecesis in them must rest upon reproduction.

Ecesis in bare areas.—The selective action of bare areas upon the germules brought into them is exerted by ecesis. It has repeatedly been pointed out that the essential nature of such areas is found in the water relations, and that it can best be expressed in the amount of departure from the climatic mean. The two extremes, water and rock, are the extremes for ecesis, the one impossible for plants whose leaves live in the air and the light, the other for those whose roots must reach water. The plants which can ecize in such extremes are necessarily restricted in number and specialized in character, but they are of the widest distribution, since the habitats which produced them are universal. From the standpoint of ecesis, succession is a process which brings the habitat nearer the optimum for germination and growth, and thus permits the invasion of an increasingly larger population. The fundamental reason why primary succession is long in comparison with secondary lies in the fact that the physical conditions are for a long time

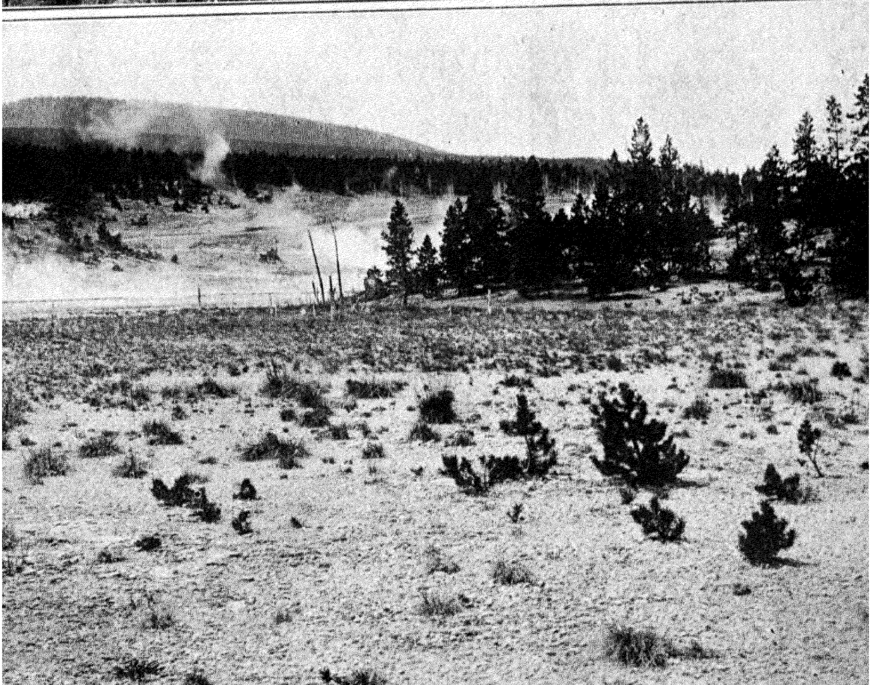
too severe for the vast majority of migrants, as well as too severe for the rapid increase of the pioneers. Secondary soils, on the contrary, afford more or less optimum conditions for germination and growth, and are invaded and stabilized with corresponding rapidity (plate 9, A. B).

COMPETITION.

Nature.—Competition occurs whenever two or more plants make demands in excess of the supply (Clements, 1904:166; 1905:285; 1907:251). It is a universal characteristic of all plant communities, and is absent only in the initial stages of succession, when the pioneers are still isolated. It increases with the increase of population in successive stages until the climax or sub-climax is reached, after which it decreases again with the population. It is necessarily greatest between individuals or species which make similar or identical demands upon the same supply at the same time, and least or quite lacking in associated plants with demands largely or quite unlike.

In its essential nature, competition is a decrease in the amount of water and light available for each individual, or for each species as represented by the total number of individuals. It affects directly these two factors, and through them the response of each plant. In a few cases, such as occur when radish seeds are planted closely, it is possible to speak of mechanical competition or competition for room. The crowding of the swelling roots is, however, only an incident in the competition for water, and seems to have no counterpart in nature. There is no experimental proof of mechanical competition between root-stocks in the soil, and no evidence that their relation is due to anything other than competition for the usual soil factors—water, air, and nutrients.

Competition and dominance.—Properly speaking, competition exists only when plants are more or less equal. The relation between host and parasite is not competition, nor is that between a dominant tree and a secondary herb of the forest floor. The latter has adapted itself to the conditions made by the trees, and is in no sense a competitor of the latter. Indeed, as in many shade plants, it may be a beneficiary. The case is different, however, when the seedlings of the tree find themselves alongside the herbs and drawing upon the same supply of water and light. They meet upon more or less equal terms, and the process is essentially similar to the competition between seedlings alone on the one hand, or herbs on the other. The immediate outcome will be determined by the nature of their roots and shoots, and not by the dominance of the species. Naturally, it is not at all rare that the seedling tree succumbs. When it persists, it gains an increasing advantage each succeeding year, and the time comes when competition between tree and herb is replaced by dominance and subordination. This is the course in every bare area and in each stage of the sere which develops upon it. The distinction between competition and dominance is best seen in the development of a layered forest in a secondary area, such as a burn. All the individuals compete with each other at first in so far as they form intimate groups. With the growth of shrubs, the latter become dominant over the herbs and are in turn dominated by the trees. Herbs still compete with herbs, and shrubs with shrubs, as well as with younger individuals of the next higher layer. Within the dominant tree-layer, individuals compete with individuals and species with species. Each layer exemplifies the rule that plants similar in demands compete when in



A. Ecesis in a primary area, summit of Pike's Peak, Colorado.
B. Ecesis in a secondary area denuded by hot water, Norris Geyser Basin, Yellowstone Park.

the same area, while those with dissimilar demands show the relation of dominance and subordination.

Competition in air and in soil.—The competition between pioneers is usually restricted to the soil, where the roots compete with each other for water. It is often also the simple competition typical of families, in which all the individuals make identical demands because they belong to one species. As the families become communities by extension or by migration, the competition becomes more complex and the outcome in many cases is dominance. This is particularly true as the bare area becomes covered, and success in ecesis comes to depend upon the ability to overshadow other plants. The taller plant gradually gains the upper hand, partly because it receives more light and makes more growth, and partly because its demands are increased by greater transpiration. At the same time the shorter plant receives less light, grows and transpires less, and its needs for water diminish. This interplay of competition and reaction occurs in all communities with individuals of different height and extent, but in varying degrees. In pure grassland, competition of the roots for water is controlling, and the aërial shoots compete slightly or not at all. Where broad-leaved herbs play an important or characteristic part, shoots compete with each other for light. This is true of typical prairie to such a degree that actual layers come to be developed, as occurs also in other grassland. From the competition in the prairie to that of the scrub and the forest is but a change of degree. The dominance of the trees is only the outcome of a competition in which position means the control of light, and thus of water. Competition of shoots alone may occur when the water-supply is in excess, and hence competition for water is absent. This is most evident in the case of submerged plants.

Woodhead (1906) distinguishes communities as *competitive* when the dominants occupy the same soil layer, and *complementary* when the roots are in different layers. It is one of the most important tasks of ecology to determine the root and shoot relations of communal plants, but it seems much better to apply Woodhead's terms to the species concerned and not to the whole community. It is the species which are competitive or complementary, and not the community. Moreover, species which are complementary as to roots may be competitive as to shoots, and *vice versa.* In addition, the individuals of each species are competing more or less actively, and this is the case with the secondary species also, both as to themselves and the dominants. Finally, the complementary relation in many cases, if not in all, is merely the outcome of the more or less complete success of certain species by which competition is changed into dominance. Our knowledge of both competition and dominance at present is quite too rudimentary to warrant drawing distinctions, except as suggestive working hypotheses.

Rôle of competition in succession.—As already indicated, competition affects the amount of water and of light, even to the point of complete control when success in competition becomes dominance; hence its effect upon ecesis is direct and often critical. It is seen in the behavior of the seedlings of species already in possession, as well as in that of new invaders. Competition is most decisive during the development of the seedling and at the time of reproduction, particularly in the case of perennials and woody plants. Accordingly it plays a large part in determining the relative number of occupants

and invaders in each stage of a sere, and thus helps to control the course of development. In analyzing the rôle of competition in the latter, it is desirable to distinguish the simple competition of the members of a family and the competition of the individuals of a single dominant of the primary or other layer from the competition between dominant species or that of secondary species. As we have seen, the competition between dominant and secondary species has ceased and is replaced by a relation of dominance and subordination. The reaction of a plant community upon its habitat is largely the sum of the habitat effects of competition and dominance. The latter is paramount, however, and is chiefly or solely concerned in most important reactions.

The general effect of competition upon succession has already been indicated. Its influence may be sketched in some detail by tracing the primary development of a spruce forest in brief. The initial crustose lichens which colonize the bare rock usually compete with each other little or not at all. With the invasion of foliose forms, the competition of the two begins, often ending in the complete dominance of foliose *Parmelias*, etc. The latter compete with each other more or less vigorously, even when they occur on the rock disintegrated into gravel. Their stabilizing reaction upon the gravel-slide aids the invasion of pioneer phanerogams, but there is no competition between these and the lichens, even in the case of seedlings. This is naturally because of the extreme dissimilarity of their demands. Competition appears again only as the result of the slow aggregation of individuals into families and colonies, and is rarely if ever an important feature of this open stage. With the entrance of a large number of sub-pioneers, the number of individuals increases rapidly, and competition for water is often acute. The result is that the pioneers disappear rapidly and usually completely. The appearance of perennial grasses increases the competition of the half-gravel stage, and often translates it into dominance, the resulting grassland acting as a subclimax. Often, however, shrubs or aspens enter before the grasses become controlling, and the intense competition which results passes into a dominance based on light-control. The development of the pine stage is regularly conditioned by the reactions of the shrubs. The latter and the young pines compete with each other more or less actively for a time, but the pines ultimately secure partial dominance at least. When the dominance is complete, the pines compete vigorously with each other and produce a light reaction unfavorable to the ecesis of their seedlings, but favorable to the seedlings of the spruce and fir. The latter succeed in the constant competition during seedling and sapling stage, and take their place in the primary layer as codominants. The pines decrease in number, probably more from the failure of reproduction than from competition with the adult spruces and firs. They eventually disappear completely or are represented only by an occasional relict.

While the control of the climax species is now secure except for accidents, competition still goes on between the adults as well as the seedlings of each year, resulting in oscillations in number. It is still a progressive process with the members of the different layers of the undergrowth as the amount of light steadily decreases, and it ceases only with the disappearance of the layers caused by the growing absorption of the canopy. During this time, however, a secondary effect of competition and dominance is seen in the seasonal aspects

typical of the undergrowth. The appearance of the species of each layer is controlled by competition and dominance in such fashion that the layers below the dominant one develop in the order of position, the lowermost first, before the shrubs have developed their foliage. This effect is of course seen most clearly in the aspects of deciduous forests, in which the lowest layer consists chiefly or wholly of prevernal or vernal species. A similar and sometimes equally conspicuous sequence of layers occurs in prairies.

INVASION.

Nature and rôle.—Invasion is the complete or complex process of which migration, ecesis, and competition are the essential parts (Clements, 1904: 32; 1905:210; 1907:270). It embraces the whole movement of a plant or group of plants from one area into another and their colonization in the latter. From the very nature of migration, invasion is going on at all times and in all directions. For our purpose it is necessary to distinguish between invasion into a bare area and into an existing plant community. The former initiates succession, the latter continues the sere by producing successive stages until the climax is reached. Invasion does not cease at this point necessarily, especially in the presence of artificial processes. As a rule, however, invasion into a climax community is either ineffective or it results merely in the adoption of the invader into the dominant population. From the standpoint of succession only those invasions need be considered which people bare areas or produce a new developmental stage. It is obvious that practically all invasion in force is of this sort.

Effective invasion is predominantly local. It operates in mass only between bare areas and adjacent communities which contain species capable of pioneering, or between contiguous communities which offer somewhat similar conditions or contain species of wide range of adjustment. Invasion into a remote region rarely has any successional effect, as the invaders are too few to make headway against the plants in possession or against those much nearer a new area. An apparent exception is found in the case of ruderals introduced into new countries by man, but these rarely come to be of importance in succession until they have been domiciled for many years. The invasions resulting from the advance and retreat of the ice during glacial times were essentially local. They spread over large areas and moved long distances only as a consequence of the advance or withdrawal of the ice. The actual invasion at any one time was strictly local. Invasion into a new area or a plant community begins with migration when this is followed by ecesis. In new areas, ecesis produces reaction at once, and this is followed by aggregation and competition, with increasing reaction. In an area already occupied by plants, ecesis and competition are concomitant and quickly produce reactions. Throughout the development migrants are entering and leaving, and the interactions of the various processes come to be complex in the highest degree.

Kinds of invasion.—Local invasion in force is essentially *continuous* or *recurrent*. Between contiguous communities it is mutual, unless they are too dissimilar. The result is a transition area or ecotone which epitomizes the next stage in development. By far the greater amount of invasion into existing vegetation is of this sort. The movement into a bare area is likewise continuous, though it is necessarily not mutual, and hence there is no ecotone

during the earlier stages. The significant feature of continuous invasion is that an outpost may be repeatedly reinforced, permitting rapid aggregation and ecesis, and the production of new centers from which the species may be extended over a wide area. Contrasted with continuous invasion is intermittent or periodic movement into distant regions, but this is rarely concerned in succession. When the movement of invaders into a community is so great that the original occupants are driven out the invasion is *complete*. This is characteristic of the major stages of succession, though there are necessarily transitions between these, often of such character as to require recognition. Major stages, and especially subclimaxes and climaxes, often undergo *partial* invasion without being essentially changed. While the permanence of invasion varies greatly, the terms "permanent" and "temporary" are purely relative. In each sere initial and medial stages are temporary in comparison with the climax. The initial stages of a primary sere may last for centuries, but they must finally pass in the course of development. Climax stages are permanent, except in the case of destruction or an efficient change of climate. In the geological sense, however, they are transient stages of the geosere.

Manner of invasion.—Bare areas present very different conditions for invaders to those found in plant communities. This is due to the absence of competition and often of reaction. Conditions for germination are regularly more favorable in plant communities, but the fate of seedling and adult is then largely determined by competition. Open communities are invaded readily, closed ones only with difficulty, if at all. It is important to recognize that a community is not necessarily open because part of the surface is bare. Secondary bare areas usually afford maximum opportunity for invasion. This is due partly to the lack of competition, but especially to the fact that conditions are more or less optimum for the germination and growth of a wide range of species. Primary areas, on the contrary, present only extremes of water-content, and thus exclude all invaders except a few pioneers.

Invasion into a bare area may be lateral, peripheral, or general. It is lateral in all land areas bordered by deep water, since successful invaders can reach it only from land communities. It may be bilateral when the water is shallow enough to contain amphibious species and the area sufficiently wide to permit a gradual change of conditions. When the bare area lies between two different terrestrial associations the movement is regularly from both directions, if conditions are not too extreme. If it is surrounded by an association or associes, but particularly the former, the invasion takes place all along the edge. When the area is large the invaders move forward into it by repeated advances, often producing temporary zones. In small areas such a zonal invasion is typical when species invade by propagules. In many secondary areas, especially burns and abandoned fields, the migration is general, and the area is more or less completely covered in the initial stage.

In all invasions after the first or pioneer stage, the relative level of occupants and invaders is critical. A community may be invaded at its level, *i. e.*, by species of the same general height as those in occupation, or below or above this level. When invasion is at the same height, the level has no effect and the sequence is determined by other features. If it is above the level of the occupants, the newcomers become dominant as they stretch above their

neighbors and soon give character to a new stage. This is typically the case with shrubs and trees, in which the close dependence of the sequence of stages upon life-form is most evident. When invasion is below the existing level, it has no direct influence upon the dominant species. Such invaders normally take a subordinate place as secondary components of the community. In rare instances they play an important or decisive part by virtue of some advantageous competition form, such as the rosette or mat, or of some unique reaction, as in *Sphagnum*.

Barriers.—A topographic feature or a physical or a biological agency that restricts or prevents invasions is a barrier. Topographic features are usually permanent and produce permanent barriers. Biological ones are often temporary and exist for a few years or even a single season. Temporary barriers are often recurrent, however. Barriers are complete or incomplete with respect to the thoroughness of their action. They may affect invasion either by limiting migration or by preventing ecesis. It has been generally assumed that their chief effect is exerted upon migration, but it seems clear that this is not the case. Even in the case of extensive barriers, such as the ocean, the influence upon ecesis is decisive.

Barriers are physical when due to some marked topographic feature, such as an ocean, lake, river, mountain range, etc. All of these are effective by virtue of their dominant physical factors. They prevent the ecesis of the species coming from very different habitats, though they may at the same time serve as conductors for plants from similar habitats. This is especially true of water-currents and mountain ranges. A body of water with its excessive water-content is a barrier to mesophytes and xerophytes, but a conductor for hydrophytes. Deserts set a limit to the invasion of mesophytic and hydrophytic species, while they favor that of xerophytes. By its reduction of temperature, a high mountain range restricts the extension of plants of lowlands and plains. It is also more of an obstacle to migration than most physical barriers, because of the difficulty of movement up its slopes. Any bare area with extreme conditions is a barrier to the invasion of communities beyond. It is not to be regarded as a barrier to the development of succession upon it, since the proper pioneeers are always able to invade it.

Biological barriers.—Biological barriers comprise plant communities, man and animals, and parasitic plants. The limiting effect of a plant community is exhibited in two ways. In the first place, an association acts as a barrier to the ecesis of species invading it from associations of another type, on account of the physical differences of the habitats. Whether such a barrier be complete or partial will depend upon the relative unlikeness of the two areas. Shade plants are unable to invade a prairie, though the species of open thickets or woodland may do so to a certain degree. A forest formation, on account of its diffused light, is a barrier to poophytes, while a swamp, because of the amount and kind of water-content, sets a limit to the species of both woodland and grassland. Such formations as forests and thickets act also as direct obstacles to migration in the case of tumbleweeds and other anemochores, clitochores, etc. Closed communities likewise exert a marked influence in decreasing invasion by reason of the intense and successful competition which all invaders must meet. Closed associations usually act as complete barriers, while more open ones restrict invasion in direct proportion to the

degree of occupation. To this fact may be traced the fundamental law of succession that the number of stages is determined largely by the increasing difficulty of invasion as the area becomes stabilized. Man and animals affect invasion by the destruction of germules. Both in bare areas and in seral stages the action of rodents and birds is often decisive to the extent of altering the whole course of development. Man and animals operate as marked barriers to ecesis wherever they alter conditions unfavorably to invaders or where they turn the scale in competition by cultivation, grazing, camping, parasitism, etc. The absence of pollinating insects is sometimes a curious barrier to the complete ecesis of species far out of their usual habitat or region. Parasitic fungi decrease migration in so far as they affect seed production. They restrict or prevent ecesis either by the destruction of invaders or by placing them at a disadvantage with respect to the occupants.

Changes in barriers.—A closed formation, such as a forest or meadow which acts as a decided barrier to invasion, may disappear completely as the result of a land-slide, flood, or burn, and leave an area into which invaders crowd from every point. A temporary swing of climate may disturb the balance of a community so that it permits the entrance of mesophytes which are normally barred, and one or more stages of succession may be omitted as a consequence. On the other hand, a meadow or swamp, for example, ceases to be a barrier to prairie xerophytes during a period of unusually dry years, such as regularly occurs in semiarid regions. A peculiar example of the modification of a barrier is afforded by the complete defoliation of aspen forests in the Rocky Mountains. As a result, they were invaded by poophytes, producing a change of development identical with that found in the usual aspen clearing. Nearly all xerophytic stretches of sand and gravel, dunes, blow-outs, gravel-slides, etc., as well as prairies and plains in some degree, exhibit a recurrent seasonal change in the spring. As a result, the dry, hot surface becomes sufficiently moist to permit the germination and growth of invaders, which are normally barred out during the rest of the year. The influence of distance as a barrier has already been indicated under "Migration."

V. REACTIONS.

Concept and nature.—By the term *reaction* is understood the effect which a plant or a community exerts upon its habitat (Clements, 1904:124; 1905: 256; 1907:282). In connection with succession, the term is restricted to this special sense alone. It is entirely distinct from the response of the plant or group, *i. e.*, its adjustment and adaptation to the habitat. In short, the habitat causes the plant to function and grow, and the plant then reacts upon the habitat, changing one or more of its factors in decisive or appreciable degree. The two processes are mutually complementary and often interact in most complex fashion. As a rule, there is a primary reaction with several or many secondary ones, direct or indirect, but frequently two or more factors are affected directly and critically. Direct reactions of importance are confined almost wholly to physical factors, with the exception of parasitism, which can hardly be regarded as a reaction proper. With almost no exceptions, reactions upon biological factors have barely been touched by investigators as yet. Any exact understanding of them must await the quantitative study of the community as a biological unit.

The reaction of a community is regularly more than the sum of the reactions of the component species and individuals. It is the individual plant which produces the reaction, though the latter usually becomes recognizable through the combined action of the group. In most cases the action of the group accumulates or emphasizes an effect which would otherwise be insignificant or temporary. A community of trees casts less shade than the same number of isolated individuals, but the shade is constant and continuous, and hence controlling. The significance of the community reaction is especially well shown in the case of leaf-mold and duff. The leaf-litter is again only the total of the fallen leaves of all the individuals, but its formation is completely dependent upon the community. The reaction of plants upon wind-borne sand and silt-laden waters illustrates the same fact.

Some reactions are the direct consequence of a functional response on the part of a plant. This is exemplified by the decrease of water-content by absorption, the increase of humidity as a consequence of transpiration, and the weathering of rock by the excretion of carbon dioxid. Others are the immediate outcome of the form or habit of the plant body. The difference between woody plants and grasses in the reaction upon light and humidity is one of the critical facts in succession. Almost any obstruction may cause the deposition of dune-sand or of water-borne detritus. The actual formation of a dune depends, however, upon the aërial and soil forms so typical of sand-binders. The accumulation of leaf-mold, filling with plant remains, and the production of humus are all due to the death and decay of plants and plant parts. Marl, travertine, calcareous tufa, and sinter are partly or wholly the result of little-understood processes of the plant. The successful reaction of pioneers in gravel-slides and in bad lands is almost wholly a matter of mat, rosette, or bunch forms and of extensive or deep-seated roots. In a primary area the reaction is exerted by each pioneer alone, and is then augmented by the family or colony. It extends as the communities increase in size, and

comes to cover the whole area as vegetation becomes closed. It is often felt for a considerable space around the individual or group, especially when exerted against the eroding action of wind or water, or the slipping consequent upon gravity. In most secondary areas and seral stages the reaction is the combined effect of the total population. In it the preponderant rôle is played by successful competitors and particularly by the dominants. These determine the major or primary reactions, in which the part of the secondary species is slight or negligible.

Rôle in succession.—In the development of a primary sere, reaction begins only after the ecesis of the first pioneers, and is narrowly localized about them and the resulting families and colonies. It is necessarily mechanical at first, at least in large degree, and results in binding sand or gravel, producing finely weathered material, or building soil in water areas, etc. In secondary seres, extensive colonization often occurs during the first year and reaction may at once be set up throughout the entire area. The reactions of the pioneer stage may be unfavorable to the pioneers themselves, or they may merely produce conditions favorable for new invaders which succeed gradually in the course of competition, or become dominant and produce a new reaction unfavorable to the pioneeers. Naturally, both causes may and often do operate at the same time. The general procedure is essentially the same for each successive stage. Ultimately, however, a time comes when the reactions are more favorable to occupants than to invaders, and the existing community becomes more or less permanent, constituting a climax or subclimax. In short, a climax vegetation is completely dominant, its reactions being such as to exclude all other species. In one sense, succession is only a series of progressive reactions by which communities are selected out in such a way that only that one survives which is in entire harmony with the climate. Reaction is thus the keynote to all succession, for it furnishes the explanation of the orderly progression by stages and the increasing stabilization which produces a final climax.

Previous analyses of reaction.—The essential nature of reaction has been little recognized in the past, and there have been but two attempts to analyze and group the various reactions. Clements (1904:124; 1905:257; 1907:282) pointed out that the direction of movement in succession was the immediate result of its reaction, and that the latter is expressed chiefly in terms of water-content. He further stated that the initial causes of succession must be sought in the physical changes of the habitat, but that the continuance of succession depended upon the reaction which each stage exerted upon the habitat. The general reactions of vegetation were classified as follows: (1) preventing weathering, (2) binding aeolian soils, (3) reducing run-off and preventing erosion, (4) filling with silt and plant remains, (5) enriching the soil, (6) exhausting the soil, (7) accumulating humus, (8) modifying atmospheric factors, light, humidity, etc. Cowles (1911:173) has classified plant and animal agencies in succession in five groups: (1) humus complex, (*a*) water, (*b*) soil organisms, (*c*) toxicity, (*d*) food, (*e*) temperature and aëration; (2) shade; (3) plant invasion; (4) man; (5) plant plasticity. The factors of the humus complex and shade are reactions, as the term is understood here. Invasion is the basic process of which succession is but the continuance or recurrence; man is an initial cause, and plasticity a response to the habitat as modified by reaction.

Kinds of reactions.—Since two or more major reactions regularly occur in a primary sere, and in many secondary ones also, it is impossible to classify them on a strictly developmental basis. It is most convenient to group them in accordance with their nature and effect, an arrangement which is likewise fundamental because it emphasizes the directive influence of reactions. While it is helpful to distinguish them as primary and secondary with respect to a particular sere, such a general distinction is not feasible, owing to the fact that a reaction may be primary in one sere and secondary in another, or in different periods of the same sere. The main division may well be made upon the seat of the reaction, which results in the two groups, (1) soil reactions and (2) air reactions. The soil as a fixed substratum is much more affected by plants, and the soil reactions are correspondingly much more numerous than those in the air. They do not permit of any precise subdivision, since soil factors are so intimately related. It is helpful in permitting a comprehensive view to group them in accordance with the factor directly affected. This results in the following arrangement: (1) soil formation and structure, (2) water-content, (3) solutes, (4) soil organisms. The subdivision of air reactions is less satisfactory, but the following will serve our present purpose: (1) light; (2) other factors (humidity, etc.); (3) aërial organisms.

In the following discussion of reactions in detail, an endeavor is made to indicate the cause of each reaction, to trace its effect upon the habitat, and to relate this to the development of the succession. Some of the recent quantitative studies of reactions are also indicated. The exact study of this most difficult portion of the field of succession has barely begun, and the many gaps in our knowledge are consequently not surprising.

SOIL FORMATION.

Manner.—The reactions of plants upon the substratum fall into two categories, viz, (1) those which produce a new substratum or soil and (2) those which affect and usually change the texture of the soil.

A new substratum may be formed in four essentially different ways: (1) by the accumulation of the plant bodies themselves, usually under conditions which retard or prevent decay; (2) by the concretion of mineral matters into rock or marl through the activity of water plants; (3) by the weathering of rock into fine soil by the excretion of acids; (4) by the resistance which plant bodies offer to moving air and water, resulting in the deposition of particles in transport. Plants modify the structure of the soil primarily as a result of the death and decay of plant bodies and parts, a reaction differing from the accumulation of plant remains into a new soil only in the degree of accumulation and of decay. They also affect soil-texture in consequence of the penetration of their roots and the accompanying liberation of carbon dioxid, but this effect hardly seems a significant one. The most striking reaction upon soil-structure occurs in the formation of a rocky layer termed "ortstein" from the typical "bleisand" of many heaths. Another group of reactions affect the soil by preventing weathering, or the erosion of the surface by wind and water.

(1) *Reaction by accumulating plant bodies or parts.*—The complete decomposition of plants in contact with air prevents any considerable heaping-up of plant remains in ordinary habitats. Accumulation in quantity can occur in consequence only under water, where oxidation is largely or completely

prevented. This is the universal method by which biogenous soils are formed, thought it must be recognized that animals also usually play a large or controlling part in the process. As a reaction proper it is brought about only by plants which grow in water or in wet places, but the formation of the soil may be hastened by the incorporation of transported material, including terrestrial plants as well as animal remains and detritus. It is the characteristic reaction of aquatic and amphibious communities, and occurs in salt water as well as in fresh water. The peat substratum which results is found universally wherever plants decompose in the presence of insufficient oxygen. As is well known, a similar process has recurred throughout geological history, resulting in the formation of coal at various times from the Paleozoic to the Tertiary. Along with the biogenous formation of the soil occur certain secondary consequences, such as the production of acids, of possible toxic substances, changes in soil organisms, etc., which are considered elsewhere.

The shallowing of water by pioneer aquatics first changes the conditions to the detriment of submerged plants and the advantage of floating species, and then to the respective disadvantage and advantage of floating and amphibious plants. This is equally true when water-borne detritus plays a part, for it merely hastens the outcome. The process is continued by the amphibious reeds and sedges, which may yield finally to meadow grasses. In this stage, surface-water usually disappears, and the accumulation ceases entirely or nearly so, because of the access of oxygen. In boreal and mountain regions *Sphagnum* usually enters in the amphibious stage or near its close, and gives a new lease to accumulation under circumstances which may almost completely inhibit decomposition. After a time the moss layer becomes so thick that other plants may enter because of the decreasing water-content of the surface, which controls the further development. *Sphagnum* may also extend as a floating mat over pools and ponds, and eventually fill them with peat (plate 10 A).

A host of investigators have studied the formation of soil by peat-producing plants (Plant Succession, pp. 238, 378). Various kinds of peat have been distinguished on the basis of the component species and the degree of decomposition and compression. These have little bearing on the reaction here considered, since the mere accumulation is the chief fact. The direct reaction which influences the sequence of stages is, however, the change in water depth and content incident to the increase of thickness of the peat. In the submerged and floating stages the directive factor is the decreasing depth which permits the entrance of species with floating leaves. Such plants cut off the light from the submerged pioneers and probably change other conditions unfavorably also. A further reduction of depth allows the ecesis of amphibious reeds, and these first dominate and then displace the floating plants, partly, it seems, in consequence of light reduction. From this point the essential change is a decrease of water-content, largely by continued filling but partly because of the relative increase in transpiration. This is the ruling reaction throughout the rest of the development, unless the latter is deflected by the appearance of *Sphagnum*, or until it reaches the shrub or forest stage.

The formation of soil by the deposition of diatom shells is relatively insignificant, though frequently found on a small scale. It probably played a larger part in the geological past, if one may judge from the existence of extensive diatom beds in various places in Nebraska, California, Nevada, etc.

While the production of diatomaceous soil may be seen along the margins of many pools and streams, diatom marshes of large extent are rare. Weed (1887) has traced their development in Yellowstone Park, and has found that extensive meadows have been built up in this way. In spite of the difference of material and the absence of certain secondary influences, the primary reaction has to do with the decrease in the amount of water, as in the case of peat areas.

(2) *Reaction by accumulating plant concretions.*—The rocky substrata due to the direct physiological activity of plants are either calcareous or siliceous, the former being much more common. Calcareous substrata are represented by marl, travertine, calcareous tufa and perhaps by oölite; siliceous ones by sinter or geyserite. Concretions of either sort are usually formed by algæ and are especially characteristic of hot springs. Aquatic mosses also possess the power of secreting travertine and tufa. *Chara* plays the chief rôle in the formation of marl (Davis, 1900, 1901), while Rothpletz (1892) assumes that oölite is due to the calcareous secretions of a blue-green alga. Cohn (1862) was the first to point out the connection of algæ with the formation of tufa and sinter. The first studies of importance in this country were made by Weed (1889) in Yellowstone Park, and these have been supplemented by those of Tilden (1897, 1898) in the Rocky Mountain region generally. Tilden has described 24 algæ from the hot springs of this region, and it is probable that all of these play a part in rock formation. The yellow-green algæ (Chlorophyceae) are represented by *Oedogonium, Hormiscia, Conferva, Microspora, Rhizoclonium,* and *Protococcus.* The blue-green thermal algæ (Cyanophyceae) belong to the genera *Calothrix, Rivularia, Hapalosiphon, Schizothrix, Symploca, Phormidium, Oscillatoria, Spirulina, Synechococcus, Gloeocapsa,* and *Chroococcus.* In the case of the marl or lime deposit of lakes, Davis finds that it is made up of coarser and finer material derived from the incrustations on *Schizothrix* and *Chara,* but principally the latter.

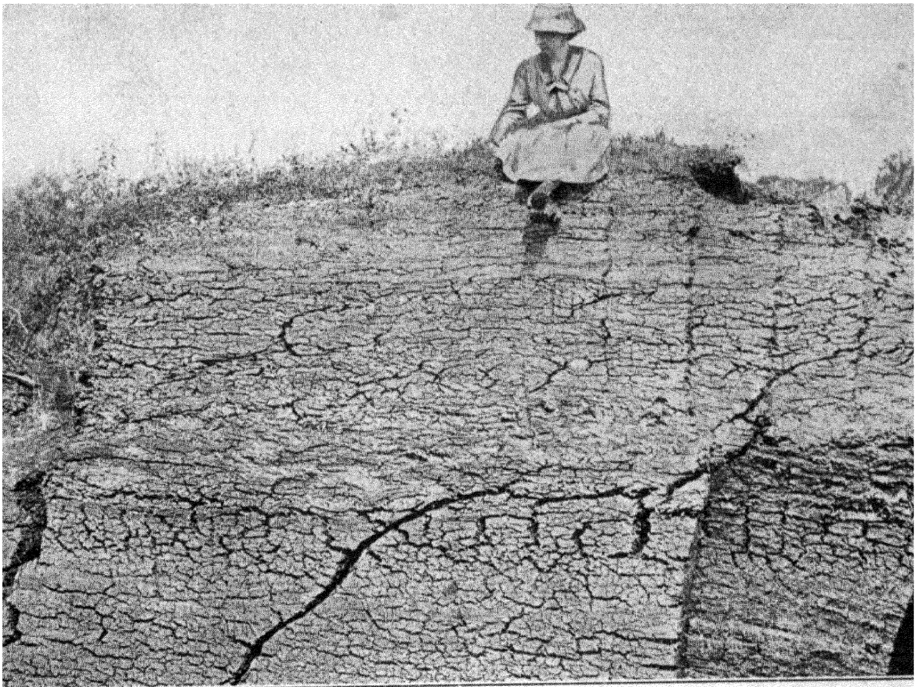
From the standpoint of succession, concretion into solid rock is very different from that by which marl is produced. The compactness of travertine, sinter, and oölite is doubtless due to the microscopical size of the algæ concerned. In the case of marl formed largely by *Chara,* the stem and leaves of the latter are so large relatively that their death and decay breaks up the concretions in large degree. The fragile branching stems and leaves also prevent compacting into a solid mass. Marl, moreover, accumulates in ponds and lakes, where its action is to shallow the water and to produce much the same results already noted for peat and diatom soils. In fact, the action is essentially identical so far as the initiation of the water sere and the direction of the first stages are concerned. Sinter and travertine are formed locally as superficial deposits under conditions which are unfavorable to colonization, though this does begin at the edges of the cooler brooks which drain the hot-spring areas. The essential fact, however, is that they are biogenic rocks and can only form initial areas for primary succession, instead of directing the sequence of stages. As in the case of tufa and oölite, the reaction of the concretionary algæ leads to the origin of a new rock sere, while in the formation of marl by *Chara* it continues and directs a water sere already begun (plate 22A).

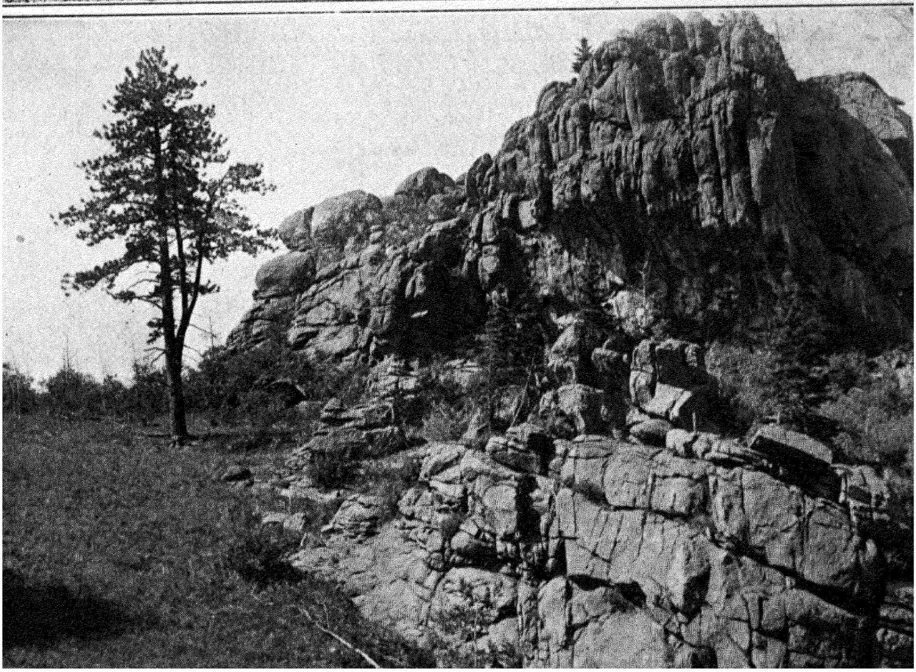
(3) *Reaction by producing weathering.*—The primary reaction of plants upon rocks is the decomposition of the surface into an exceedingly fine soil.

A secondary influence is the production and widening of cracks by means of roots and stems, but this is often lost sight of in the greater effects of atmospheric weathering. It is also impossible in many cases to separate the effect of plants and atmosphere in the intimate decomposition of rock surfaces. As a rule, however, the paramount action of the plants is indicated by its localization upon certain surfaces or areas. All pioneers on rocks break down the surface in consequence of their excretion of carbon dioxid or other acids, and produce a fine layer of dust. In the case of lichens and many mosses this layer remains in place, but usually it is carried into cracks and crevices. This slow production of a thin soil or shallow pocket is reinforced by the decay of the pioneers themselves, which also materially increases the nutrient-content and the water-holding capacity. Here, again, it is almost impossible to separate the two reactions; but this is immaterial, since their effect is the same. The combined effect is to produce areas in which rock herbs can secure a foothold and to increase slowly the water-content and the nutrient-content.

The reaction through weathering takes place most readily when the rock is sedimentary and soft, especially if it is wet or moist during a large part of the growing-season. In such places, the pioneers are mostly mosses and liverworts, often preceded by algæ. Lichens are much less frequent and are apt to be collemaceous. Water is abundant, and the effect is chiefly to produce a foothold for herbs, apart from the increase of humus. As a consequence, the pioneer stages are often extremely short, and the rocky surface may be quickly covered with herbaceous or even shrubby vegetation. When the rock is exposed to wind and sun, and especially when it is igneous, biogenous weathering begins with the crustose lichens. The influence is exerted at the contact of thallus and rock, but the corroding carbon dioxid and other secretions act also beyond the margin of the thallus during moist periods. This permits the slow extension of each thallus and the starting of new ones, with the result that the rock surfaces with upward or north to east exposure become completely incrusted. The centers of the older thalli sooner or later die and begin to break up, leaving an area of greater water-retaining capacity for the invasion of foliose lichens. By their greater size and vigor these extend more rapidly, gradually covering the crustose species and causing them to die as a result of the decrease of water and of light. The size and thickness of the foliose thallus enable it to retain water better, and thus to enhance its power to weather the surface to greater depths. The surface is usually rough and uneven by reason of folds, soredia, etc., and this helps materially in retaining the water, as well as in providing lodging-places for the spores of mosses. In their turn the foliose thalli break up at the center and offer a favorable field for the invasion of mosses and, more rarely, of low, matlike herbs. In the weathering of the granites and other hard rocks of the Rocky Mountains such herbs follow the mosses and form the fourth stage. In both stages the amount of soil steadily increases, and with it the amount of water. The disappearance of the mosses is apparently due to the change of light intensity and to the root competition of the herbs. The herbaceous mats form almost ideal areas for the colonization of large herbs and grasses, especially at the center, where they first die and decay (plate 10B).

(4) *Reaction upon wind-borne material.*—This is the reaction which results in the formation of dunes and sand-hills, and probably also of deposits of





A. Reaction by the accumulation of plant remains in water; peat beds, "Burton Lake," Lancashire, England.

B. Reaction by causing weathering, Pilot Knob, Pike's Peak, Colorado.

loess. It is the outcome of the retardation of air-currents by the stems and leaves of plants, especially pioneers in sand. The effect of the plant-body is twofold; it is not only a direct obstacle to the passage of grains of sand, but it also decreases the velocity of the wind and hastens the consequent dropping of its load. The same action likewise tends to prevent the wind from picking the sand up again and carrying it further. The underground parts of sand plants exert a complementary reaction by binding the sand through the action of roots and rhizones, and by developing shoots which keep pace with the rise of the surface. Certain pioneers form rosettes or mats, which hold the sand with such firmness that they cause the formation of hummocks with a height of one to many feet above the bare areas. The behavior of sand-binders has been a fruitful field of study, and there is probably no other group of plants whose reactions are so well understood (plate 1A).

The primary reaction upon wind-blown sand is mechanical. The pioneer grasses in particular stop and fix the sand and produce stable centers for invasion. This permits the entrance of other species capable of growing in bare sand, if it is not shifting actively. With the increase of individuals, however, the amount of vegetable material in the soil becomes greater, increasing the water-retention of the sand and the amount of nutrients. This is the primary reaction in sand areas after the sand-binders have finished their work of stabilization. The reaction which produced and colonized deposits of loess must have been similar. The action of plants in bringing about the dropping and temporary fixing of wind-blown dust must indeed have been almost identical. Because of their much smaller size the dust particles were much more readily compacted by the action of rainfall. For the same reason they retained more of the latter in the form of the holard, and loess areas were probably xerophytic for a much shorter time. While the development of the first stages was doubtless more rapid, each stage necessarily increased the humus and hence the water-content, though to a less significant degree perhaps than in sand. However, our knowledge of the initial stages on loess and of their reaction is obtained mostly from analogy, since no deposits of loess known to be forming at the present time have been studied critically (*cf.* Shimek, 1908:57; Huntington, 1914^2:575).

(5) *Reaction upon water-borne detritus.*—The effect of plant bodies upon material carried by water is essentially similar to that noted for eolian sand. Stems and leaves slow the current and cause the deposition of its load in whole or in part (plate 4). They also make difficult the removal of material once deposited, a task in which roots and root-stocks have a share likewise. This reaction is often associated with the deposition of sand and silt by the retardation of currents as they empty into bodies of water, but the effect of plants is usually predominant. The filling incident to this reaction has the consequences already indicated for filling by the accumulation of plant remains. In fact, both processes cooperate to decrease the depth of water wherever plants occur in an area through which detritus is carried. The decreasing depth controls the usual sequence from submerged to amphibious plants. The latter continue the process, but the movement of the water is steadily impeded as the level rises, until finally it overflows the area only at times of flood. This sets a limit to the accumulation of detritus, and the further development is controlled by decreasing water-content due to plant accumula-

tions, to transpiration, etc. Frequently the deposit of silt and subsequent heaping-up of plant materials go on more rapidly in some spots than in others, producing hummocks on which the future course of development is traced in miniature.

(6) *Reaction upon slipping sand and gravel.*—A characteristic feature of the Rocky Mountains is the steep talus-slope known as a gravel-slide. The angle of the slope is usually so great that some slipping is going on constantly, while the movement downward is materially increased after a heavy rain. The fixation of such a slope is a problem similar to that which occurs in dunes and blow-outs. The coarse sand or gravel must be stopped and held in opposition to the downward pull due to gravity. The movement is slower and is somewhat deeper-seated. Consequently, the species best adapted to gravel-slides are mats or rosettes with tap-roots or long, branching roots. The latter anchor the plant firmly and the cluster of stems or horizontally appressed leaves prevents the slipping of the surface area. Each plant or each colony exerts the stabilizing effect for some distance below its own area, owing to the fact that it intercepts small slides that start above it. The primary reaction is a mechanical one, and a large number of species invade as soon as the surface is stable. These increase the humus production and water-content, and the subsequent reaction resembles that of all dry sand or gravel areas (plate 2A).

SOIL-STRUCTURE.

The structure of the soil may be changed mechanically by plants through the admixture of plant remains, the penetration of roots, or the compacting incident to the presence of plants. Associated with these are chemical changes often of the most fundamental importance. In addition, plants react upon the soil in such a way as to protect it against the action of modifying forces, such as weathering and erosion by water or wind. None of these are simple reactions, but the mechanical effect of each may constitute a primary reaction. The opportunity for greater clearness and analysis seems likewise to warrant the consideration of their influence upon the basis of soil structure and profile.

(7) *Reaction by adding humus.*—The change in the texture of the soil due to the admixture of humus is caused by animals as well as by plants. In grassland and woodland soil, animals indeed play the chief part in the distribution of humus in the soil. The effect of the humus is much the same, however, quite apart from the fact that soil organisms work over only material which is destined to become humus at all events. All plant communities produce humus in some degree by the death of entire plants, annually or from time to time, and by the annual fall of leaves and the aërial parts of perennial herbs. The amount produced depends upon the density and size of the population and upon the rate and completeness of decomposition. It is small in the pioneer stages of a sere, especially in xerophytic situations, and increases with each succeeding stage. It reaches a maximum in mesophytic grassland and woodland, but falls off again with the decrease of population in a completely closed community.

The physical effect of humus is to make light soil more retentive of water and heavy soils more porous. Hall (1908:47) states this as follows: "Humus acts as a weak cement and holds together the particles of soil; thus it serves both to bind a coarse-grained sandy soil, and, by forming aggregates of the

finest particles, to render the texture of a clay soil more open." In general, it increases the water-content of dry, bare areas and tends to decrease the water-content of moist areas. The latter is chiefly the result of raising the level, and is often complicated by decreasing aëration and the possible production of harmful substances through partial decomposition. The effect of humus is most marked in the weathering of rock and in dry sand and gravel areas, where the action is cumulative throughout the whole course of development. The increase in the number or size of the individuals in each successive stage results in more material for humus production, and this increases the water-content steadily from the initial to the climax stage. While the holard increases, the echard also mounts from less than 1 per cent in sand and gravel to 12 to 15 per cent in loam, so that the chresard increases less rapidly than the total water-content. The ultimate effect in each stage is to favor the invasion of plants with greater water requirements, and hence with greater powers of competition and duration. They readily become dominant and their predecessors disappear or become subordinate.

The penetration of roots tends to make hard soil looser in texture and to increase the available water, while it decreases the permeability of sand and raises the holard correspondingly. It is so intimately associated with humus in its effects that it is difficult if not impossible to distinguish between them.

(8) *Reaction by compacting the soil.*—This is an indirect effect due to the reaction of the community upon the water-content. It constitutes a reaction of primary importance in the case of heath on sandy soils, and perhaps also in the "hard" lands of the Great Plains. In heath-sand the final outcome is the formation of a rock-like layer at a depth of 2.5 to 3 dm. This is the layer known as "ortstein." There is still much doubt as to the process by which it is formed, and it seems probable that it may arise in different ways. Graebner (1909) assumed the usual formation of "ortstein" to be as follows:

The humus substances characteristic of heath-sand remain in solution only in pure or in acid water, but are precipitated in the presence of the soil salts. They pass through the heath-sand almost unchanged, but are precipitated where the sand lies in contact with a substratum richer in mineral salts. Here is formed a brown layer which further accumulations of humus precipitates convert into the true "ortstein" which may reach a decimeter in thickness. The primary effect of "ortstein" is mechanical in that it stops the downward growth of roots completely. It seems to have an influence apart from this also, inasmuch as roots grow poorly even when they pass through openings in the layer. The horizontal growth of roots is also found where the layer is not sufficiently compact to prevent penetration. This effect seems to be due to poor aëration caused by a lack of oxygen.

The effect of "ortstein" upon the course of succession is to handicap deep-rooted plants, such as shrubs and trees, and to retard or prevent the appearance of the final stages. Instead of producing or favoring the progression of stages, as most reactions do, it limits development and tends to make the heath the climax association. A somewhat similar result occurs in grassland communities in arid or semiarid regions, where the penetration of water is limited to the root layer. The soil beneath becomes densely compacted into a layer known as "hardpan." As a result, deeper-rooted species are eliminated and the area comes to be dominated by the characteristic "short-

grasses" (Shantz, 1911). Both "hardpan" and "ortstein" favor the persistence of the community which produced them. "Hardpan," however, brings about the disappearance of the preceding population, while "ortstein" apparently does not appear until heath has long been in possession, since it depends upon the production of heath-sand. Another difference lies in the fact that heath is at most a subclimax, while the "short-grass" association is the final climatic stage (now shown to be subclimax; cf. p. 183).

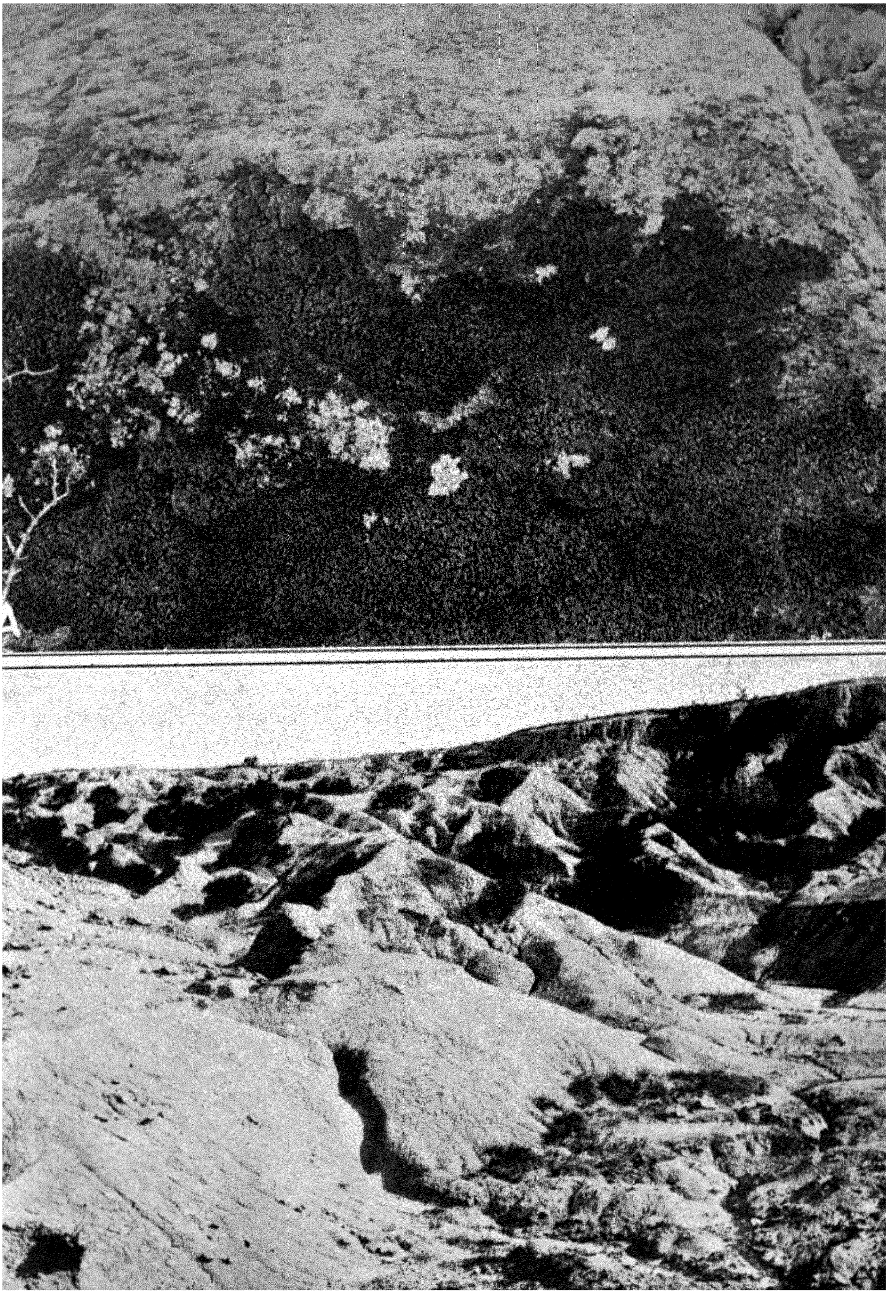
(9) *Reaction by preventing weathering or erosion.*—A plant cover, whether living or dead, everywhere produces an important reaction by protecting the surface from erosion. It has a somewhat similar effect upon the weathering of rock by atmospheric agents, but this has much less significance, since the plants themselves are producing weathering. In the case of erosion, the reaction is much the same as that which occurs when plants stop drifting sand or suspended silt. In open communities the stems and leaves reduce the velocity of wind or water and make it difficult for them to pick up soil particles; in closed associations the plants usually eliminate the effect of wind and water entirely and the erosion is null. The influence of cover is thus a progressive one, from the sparse population of the pioneer stage with most of the surface exposed to erosive action, through more and more closed communities to the climax. It is a stabilizing factor of the first importance in that it prevents denudation and consequent initiation of a new area. At the same time it assures continued occupation by the plants in possession, and hence the continuance of the reactions which produce the normal sequence of stages. The progressive increase of reaction tends to limit denudation and the renewal of succession largely to the early stages, and makes it more difficult in the final ones. Its significance is of course clearly revealed when the cover is partially or wholly destroyed (plate 11, A, B).

WATER-CONTENT.

Since water is the chief factor in succession, as in plant response, it is more or less affected by practically all reactions. In addition, the increase or decrease of water-content may be the direct outcome of the activity of the plant itself. The effect, moreover, may be exerted on the chresard as well as upon the total water-content.

(10) *Reaction by increasing water-content.*—There seems to be no case in which flowering plants increase water-content as a direct reaction. Their influence in reducing loss by evaporation from the soil is really due to the effect of shading. In the case of *Sphagnum*, however, the power of the plant to absorb and retain large amounts of rain and dew is a direct reaction of primary importance. Because of this property, *Sphagnum* is able to waterlog or flood an area and to deflect the sere or initiate a new one. In the moss areas themselves the effect is essentially to produce a new area of excessive water-content, which can be invaded only as the surface becomes drier. The ability of *Sphagnum* to retain water, either when living or in the form of peat, is also a controlling factor in the course of the development of the new sere.

The accumulation of plant remains as humus is the universal process by which the amount of water-content is increased. No plant community fails to produce humus in some degree; hence no soil escapes its action, though this is often inconsiderable in the initial stage of xerophytic areas. Its influence



A. Reaction by preventing weathering, crustose lichens, Picture Rocks, Tucson, Arizona.
B. Consocies of *Chrysothamnus* reducing water erosion in marginal gullies of bad lands, Scott's Bluff, Nebraska.

is best seen in sand and gravel, where the addition of a small amount of humus greatly increases the water-holding capacity. This is due to the minuteness of the particles of humus by which the aggregate surface for holding water is materially augmented and partly, perhaps, to a direct power of imbibing water. The total effect is to decrease loss by percolation and evaporation, and at the same time to raise the amount of non-available water. In more compact soils it increases the absorption of run-off, and possibly breaks up excessive loss by evaporation in consequence of capillarity. In the stiffest soils it also reduces the echard, correspondingly increasing the amount of water available to the plant. Humus is also associated with other reactions which affect the holard, such as weathering, preventing erosion, and protecting against evaporation.

(11) *Reaction by decreasing water-content.*—Plants decrease the holard directly only by absorption and transpiration. This is a universal reaction of plant communities, and is often critical in the case of the seedlings of woody plants. It is characteristic of the ecotone between grassland and forest, and plays an important part in the persistence of the grassland subclimaxes, as in the prairies and plains. It doubtless has a similar effect on the seres of a forest region, but its influence is much less marked. The holard is also diminished as a result of other reactions. This is most striking in the case of the shallowing of the water by plant remains and by the deposition of silt in consequence of the obstruction by vegetation.

NUTRIENTS AND SOLUTES.

The reactions of plants which affect the soil solution are least understood, and hence most debated. The actual existence of some of them is still in controversy, and in but one or two cases has a definite relation to succession been demonstrated. The possible reactions upon the content of the holard are as follows: (1) by adding nutrients or actual food, (2) by decreasing nutrients, (3) by producing acids, and (4) by producing toxins.

(12) *Reaction by adding nutrients or foodstuffs.*—This reaction is the direct consequence of the annual fall of leaves and the death and decomposition of plants or plant parts. In this way a large supply of mineral salts is returned to the soil, and sooner or later these are freed to enter the soil solution. It seems clear that this process favors plants with a high nutrient requirement, but this may be negligible where there is an abundance of nutrients in the soil. The whole question really hinges upon the relation between the amount returned each year and the amount already available in the soil. At any rate, we have no convincing evidence that humus plays an efficient rôle in succession apart from its fundamental relation to water-content. Experiment only can decide this matter, since nutrients and water are absorbed together and both would necessarily tend in the same direction. Cowles (1911:176) has suggested that glucose and other soluble food in the humus may be absorbed by green plants, but as yet there is no direct evidence of such utilization.

(13) *Reaction by decreasing nutrients.*—The inevitable effect of the absorption and use of solutes by growing plants is to decrease the total supply. Actually, however, this reduction is insignificant in nature, and probably also in cultivation. The amount absorbed each year is a very small part of the

total amount present; so much so that even cultivation may effect no appreciable reduction in 50 years, as shown by the experiments at Rothamsted (Hall, 1905:36). In addition, all the nutrients absorbed are returned sooner or later, and in most communities the annual return must nearly counterbalance the use. In any event, there is no indication at present that successsional movement is affected by the direct decrease of nutrients through absorption.

The formation of heath-sand or "bleisand" probably furnishes an example of reduction in nutrient-content as a consequence of another plant reaction. This is the formation of acids by humus. These render the mineral nutrients soluble, and the latter are then removed by the percolating water, beginning at the top. In extreme cases, little remains but quartz sand, which acquires a characteristic leaden color in consequence of the precipitation of particles of humus. Such "bleisand" represents in consequence the extreme of poverty in regard to soil nutrients. It makes the ecesis of more exacting species almost impossible, and thus secures the persistence of the heath stage for very long periods, so that it may often be regarded as a climax.

(14) *Reaction by producing acids.*—The direct reaction of plants in excreting carbon dioxid from the root surface has already been considered under "Weathering." It is probable that this bears no relation to the production of acids in the more or less partial decomposition of humus. Wherever plant remains accumulate abundantly in water or moist places, access of oxygen is difficult. The decomposition is slow and partial, and the water or soil becomes more or less acid. The acids formed are very little understood, and the process by which they are formed is likewise obscure. Lack of oxygen seems a necessary condition of their production, and the effect of the acid upon plant growth is complicated with the effect of deficient aëration. Both appear to act together in diminishing the absorptive power of roots, probably in consequence of decreased respiration. This apparently places a premium upon plants with modifications for reducing transpiration, and acid areas are usually characterized by so-called "bog xerophytes" such as *Ledum, Kalmia, Vaccinium,* etc. In spite of much recent study, the nature of bog plants is still an open question. It seems increasingly evident that most of the xeroid species of wet places are not xerophytic at all, but that a restricted group characteristic of peat-bogs, heath-moors, etc., are actual xerophytes. Even with these, however, no final solution is possible until their water requirements have been studied experimentally and their transpiration response is known. In so far as succession is concerned, the production of acid in swamps may modify the normal reaction of decreasing water-content, and mark a series of stages which dominate for a time, owing to a favorable response to poor aëration. Whenever the latter is improved by drainage, filling, or a drier climate, conditions become more favorable to species of neutral or alkaline soils, and the bog plants disappear in consequence or as the outcome of competition. The work of Gates (1914) confirms the assumption that the bog heaths are the result of winter xerophily, while a recent study of the transpiration and growth of plants in aërated bog-water indicates that the acid is a concomitant only, and not a cause.

(15) *Reaction by producing toxins.*—The question of the direct production of toxic substances by excreting plant roots is a much mooted question.

Without attempting to pass upon the matter in general, it may be said that the most persistent search for a decade has failed to reveal any evidence of their rôle in the innumerable examples of succession in the Rocky Mountains. On the contrary, the detailed study of the ecesis of occupants and invaders in the families and colonies of pioneer stages indicates better development in such areas, as would be expected from their reactions.

The existence of bog toxins resulting from partial decomposition or from the complex organic interactions of bogs is much more probable (Livingston, 1905; Transeau, 1906; Dachnowski, 1912). It is difficult to regard their presence as proved, however, and a long period of quantitative and experimental study of succession is needed to reveal their importance as a reaction. At the present it seems clear that acids, poor aëration, and bog toxins would all have the same effect upon successional movement. The chief task before us is to assign to each one its proper place (for later views, cf. Clements, 1921).

SOIL ORGANISMS.

The relation of plants to the organisms in the soil is so complex that it is impossible to recognize all of the effects, or to distinguish the causes of many of them. For the present purpose it will suffice perhaps to draw a distinction between the organisms directly connected with the plant and those not in organic relation to it. The former may be included in the general term of parasites, though many are symbiotic, of course, while the latter are saprophytes. Animals as well as plants are found in both groups. The parasites may be regarded as a direct reaction of the plants, while the saprophytes are an indirect reaction, or, better, a consequence of the accumulation of plant remains.

(16) *Reaction by means of parasites.*—The relation between host-plant and parasite is so intimate that it seems hardly to constitute a reaction. Yet it has a direct bearing upon the fate of the community and its part in succession. The latter is determined largely by the degree of parasitism. If it is intense and destructive, the individual will be destroyed or handicapped in its competition or dominance. As a consequence, it may disappear wholly from the community, though this is relatively rare. The most usual effect is a decrease in number or dominance by which the species assumes a less important rôle. In the majority of cases no direct influence is discoverable, the effect being merged in the general outcome of competition.

When the relation is more or less symbiotic, its general effect is first to increase the dominance of the host-plant, but finally to favor species with higher nitrogen demands. Warren (1909) has pointed out that this is the effect of the nodule-bearing legumes in the prairie formation. The legumes are able to grow in the poorer soils by virtue of their symbiotic partnership and consequent nitrogen production. They thus make possible the greater development of grasses, before which they disappear, sometimes completely. The presence of mycorrhiza alone makes possible the successful ecesis of an increasing number of plants, especially trees and shrubs, and hence controls their appearance in succession. Their disappearance may be due to the competition resulting from the invasion of plants with greater nitrogen demands, but it is also influenced by other reactions.

(17) *Reaction by means of saprophytes.*—These have to do chiefly with the formation of humus or with its modification in such a way as to make its nitrogen again available for plants. This is true even of those fungi which exist in the soil as saprophytes, and become parasitic when the proper host becomes available. A few of these are very destructive in their action, and sometimes effect the complete disappearance of a dominant. The fleshy fungi which play a large part in the ground layer of boreal and mountain forests have to do largely with hastening the conversion of plant remains into humus, with its attendant effects upon water-content, nutrients, etc. This is the well-known rôle of a large number of soil bacteria, especially those which free ammonia or elaborate nitrates from nitrogenous substances or fix free nitrogen. In the case of both fleshy fungi and bacteria, the final effect is to produce conditions in which plants with greater requirements can enter and displace those with less exacting demands. The same general effect is exerted by animals living in the soil, though there is some evidence that protozoa may play an antagonistic rôle.

AIR REACTIONS.

The reactions of plant communities upon atmospheric factors are less numerous and usually less controlling than those upon soil. The notable exception is the reaction upon light, which plays a decisive part in the later stages of the majority of seres. The effects upon the other air factors are so interwoven that it seems best to consider the reactions upon humidity, temperature, and wind together. As a consequence, the reactions may be grouped as follows: (1) upon light; (2) upon humidity, temperature, and wind; (3) upon the local climate; (4) upon aërial organisms.

(18) *Reaction upon light.*—The primary reaction upon light is seen in the interception of sunlight and the production of shade of varying degrees of intensity. There may also be a secondary effect upon the quality of the light (Zederbauer, 1907; Knuchel, 1914) where it has to pass through a dense canopy of leaves. The preponderance of results up to the present time indicates that the light beneath the tree-layer passes between the leaves and not through them, and is essentially unchanged as to quality. The reduction of light intensity is usually slight or even lacking in the early stages of succession, though exceptions occur whenever plants are tall and dense, as in consocies of *Phragmites, Spartina,* or *Typha,* or when leaves are broad and spreading, *Nymphaea,* etc. As the population becomes denser, it intercepts more and more light, with the result that a subordinate layer appears. With the entrance of shrubs and trees, the reaction steadily becomes more marked and the demarcation of subordinate layers more striking. In a layered forest the reduction in light value is a progressive one from the primary layer downward. In many forests of this type the cumulative reaction is so complete that the ground layer can consist only of fungi and mosses, the latter with the lowest of light requirements. As the canopy becomes denser and denser, either by the growth of individuals or by the entrance of trees with closer tops, the layers begin to disappear. This usually takes place in a downward direction, the final stage of a closed forest containing only mosses, fungi, and saprophytic phanerogams, with occasional low herbs. Thus, even

after the establishment of a dominant species of a climax stage, there may still be a successional disappearance of the subordinate layers.

The most important effect of the reaction upon light is shown in the succession of dominants after one or more have secured the controlling position with respect to light. This is seen most clearly and is best understood in the case of trees, but it is true of shrubs and in some degree of grasses and herbs. To maintain itself, a species of forest tree is confronted by the two-fold task of being able to grow in both sun and shade. If it is the first tree to invade, the crucial test comes when it has reacted upon the light in such a way as to make it necessary for its seedlings to ecize in the shade. This is a test in which practically all forest pioneers fail. The species which invade the pioneer forest must grow in reduced light intensity for a long time, until the individuals stretch above the original trees. The change of the leafy top from shade to sun is an advantage, however, and it marks the beginning of the disappearance of the trees of the first forest stage. The reaction of closer growth, denser crowns, or both, decreases the light still further, with the result that the seedlings now meet a severer test than did those of the preceding generation of the same species. In most cases they are able to establish themselves, but in smaller number and with reduced vigor. They are placed at a disadvantage in competing with the seedlings of species that endure deeper shade. When these enter they soon gain the upper hand, reach up into the dominant layer, and gradually replace the species already in occupation. In most, if not all regions with a forest climax, this process may be repeated several times, until the species whose seedlings endure the lowest light intensity are in final possession.

This succession of tree dominants was probably first clearly perceived by Dureau de la Malle (1825), but the explanation of its relation to light was first suggested by Vaupell (1857). It was long known to foresters as the "alternation of essences," and the essential response to reduced light intensity has been termed "tolerance." A table of tolerance which arranges the species of trees of the same climatic region in the order of decreasing light requirement gives also their successional relation. The earliest tolerance table was probably that of Vaupell. The first experimental determination by shading seedlings was that of Kraft (1878), which gave the following order: (1) *Pinus,* (2) *Betula,* (3) *Fraxinus,* (4) *Picea,* (5) *Acer,* (6) *Carpinus,* (7) *Fagus* and *Abies.* This table was not based upon the study of succession as was that of Vaupell. In the last decade or two various tables have been proposed on different bases for the native and exotic forest trees of Europe. For American species, Zon and Graves (1911) give a fairly complete grouping, but this does not permit a contrast of the associated species of a climax area. The most fundamental test of tolerance is perhaps the actual sequence in succession under natural conditions, supplemented by photometric determinations of light intensity in various situations. This method has given the following order for the central Rocky Mountains: (1) *Pinus murrayana;* (2) *Populus tremuloides;* (3) *Pinus ponderosa, P. flexilis;* (4) *Pseudotsuga mucronata;* (5) *Picea engelmanni;* (6) *Abies lasiocarpa* (Clements 1910).

Fricke (1904) has shown by experiment that competition for water enters into the consideration of tolerance. By cutting trenches around isolated groups of seedlings of *Pinus silvestris,* he destroyed the root competition of

the parent trees without changing the light values. In the first summer the growth of the seedlings within the area much exceeded that of those outside, while a totally new and vigorous herbaceous layer developed. He also determined the holard of soils with and without living roots, and found the latter to contain 2 to 6 times as much water. This emphasizes the influence of water-content in the later stages of succession and the degree to which competition can modify it. It also makes it plain that the more obvious effects of light in these same stages must be checked by the quantitative study of the water relations.

(19) *Reaction upon humidity, temperature and wind.*—These three factors are necessarily linked together because of their direct effect upon the plant through transpiration and the indirect effect through the evaporation of soil-moisture. The plant community reacts directly upon each factor, and these act upon each other, but the response of the plant is controlled by humidity. The reaction of a sparse pioneer population is more or less negligible, but the increasing density and height of the individuals bring about a measurable result, which becomes significant in most closed associations, especially those of shrubs and trees. In layered forests the reaction is greatest in the ground layer or beneath it, where it consists of herbs. Humidity is directly increased by transpiration, but the effect is cumulative because the moisture-laden air is not carried away. The heat rays are absorbed or reflected, and the lower temperature that results causes an increase in relative humidity. The capacity of the air for moisture is correspondingly decreased and both transpiration from the plants and evaporation from the soil-surface are reduced. The final effect is to make the water-content more efficient and thus essentially to increase it. The general effect of the reaction is the same as that of increasing humus, and the two are indistinguishable as a rule. The reduced evaporation from the surface soil, and perhaps from the seedlings as well, is a critical factor in the ecesis of many seedlings, especially those of trees.

(20) *Reaction upon local climate.*—Plant communities react upon the air above them by transpiration and by lowering the temperature. As a consequence, they receive more soil-moisture as dew and rain than do bare areas. This reaction of vegetation is measurable only in the case of forest and scrub, but probably occurs in some degree in all vegetation, particularly in the formation of dew. The effect of wooded areas upon rainfall has long been a subject of controversy, but the evidence in favor of a positive reaction is now available from so many sources that it seems conclusive. Zon (1912:205) has made the most recent summary of the evidence that forests increase rainfall. At Nancy the average increase in forested areas for 33 years was 23 per cent, while in Germany and India it was computed to be 12 per cent. A four years' experiment to check out the possible error due to faulty instruments yielded an excess of 6 per cent for the forest. Observations in the north of Germany indicate that the influence of forest increases rapidly with the altitude. At elevations less than 300 feet the effect was negligible, while at altitudes of 2,000 to 3,000 feet it ranged from 19 per cent to 84 per cent. Denuded mountains often fail to cause moisture-laden winds to precipitate their moisture, as Angot has shown to be the case in Spain. A similar influence is often exerted by the hot, dry gravel ridges about Pike's Peak upon the local showers in mid-summer.

Weber found the annual rainfall near Nancy to be 4 inches greater at a forest station than in one situated in a denuded area. Observations by Müttrich of the effect of forestation upon the rainfall of the Lüneberg heath showed that the precipitation increased steadily during a 7 years' period, and finally exceeded that of adjoining areas. Similar results were obtained after a plantation had been made in the steppes of southern Russia, where the average rainfall from 1893 to 1897 was 17.9 inches in the steppe and 22.2 inches in the newly established forest. Blandford found that the new forest growth in a protected area in British India had a decisive effect upon the rainfall, increasing it from 2 to 12 inches at various stations. Fautrat has made observations which not only show that the rainfall above tree-tops is greater than in the open, but also that it is appreciably greater above coniferous than above broad-leaved forests. These were confirmed by the rainfall recorded under broad-leaved and coniferous canopies. In 1876 the soil under the former received 16.7 inches and that under the latter only 11 inches.

Ney determined the amount of dew and frost condensed by leaves in northern latitudes to be as much as 0.4 to 0.8 inch per year. On the Pacific coast of North America and in tropical regions the condensation must be very much greater. There are no conclusive observations as to the height at which the cooling effect of a forest is felt, but Zon (219) cites the statement of Renard that this has repeatedly been noticed at an elevation of 5,000 feet during balloon ascensions.

R. von Höhnel, in the study of oak forests in Austria from 1878 to 1880, found that an acre of oak forest 115 years old absorbed from 2,200 to 2,600 gallons of water per day. This corresponds to a rainfall of 3 to 4 inches per month, or a rainfall of 17.7 inches for a vegetation period of 5 months. Zon cites also the experiments of Otozky to the effect that forest, on account of its excessive transpiration, loses more water than grassland or a bare area. He concludes that the transpiration of forests has a critical effect upon the rainfall of continents, since the amount of water consumed by a forest is nearly equal to the total annual precipitation. Brückner concluded that the vapor evaporated from the peripheral areas of continents, *i. e.*, the 79 per cent of land surface which drains directly towards the ocean, is able to supply seven-ninths of the precipitation over such areas. From the balance-sheet of water circulation over the earth's surface, Brückner reached the conclusion that 20 per cent of the vapor comes from evaporation on land, that only 7 per cent of the evaporation from the ocean reaches the land as rainfall, and that 78 per cent of all the precipitation over the peripheral land area is furnished by this area itself. While his conclusions are in accord with the facts so far as known, it is evident that their acceptance is impossible without much more exact study of evaporation and transpiration, as well as of the rainfall of many regions.

(21) *Reaction upon aerial organisms.*—As in the case of soil organisms, this may be the direct consequence of the presence of the host-plant or matrix, or it may be the indirect result of the reaction upon the air factors. As a rule, the two effects are correlated, the presence or the success of the parasitic or saprophytic organism being affected by the conditions as well as controlled by the host-plant or matrix. This reaction is characteristic of communities with a dominant canopy, such as forest and thicket, but obtains in some

degree in all vegetation. It is most obvious in the development of lichen families and colonies, and has an interesting and probably important relation to the presence and behavior of pollinating insects.

Correlation of reactions.—The efficient reactions in the great majority of seres are those that have to do with the increase or decrease of water-content and the decrease of light intensity. These are the controlling reactions in all primary seres, though a portion of the development may be dominated by the air-content or by toxins, as in peat-bogs, or by the nutrient relations, as in heath. Up to the appearance of the first shrub stage the water-content reactions are directive. With the entrance of trees and shrubs it becomes chiefly or largely subordinate to the light reactions. In the development of grass or herbaceous climax formations, reaction upon light plays a smaller part. On the contrary, many secondary seres, especially those originating in burns or clearings, may be controlled almost entirely by the decreasing light value. In short, the chief reaction upon the habitat is necessarily upon the soil and its factors, until the community develops sufficient height and dominance to control air conditions.

The accumulation of plant remains or humus is the most complex of all reactions, as it is the most universal, since it is the direct and inevitable outcome of the presence of plants. In initial water or wet areas it decreases water-content and increases nutrient-content and aëration, unless decomposition produces an excess of acids or other deleterious substances. Its effects in dry areas are largely opposite. It is the great factor in increasing the water-content, but at the same time it also increases the available nutrients. With the appearance of woody communities its influence is masked by the light reactions, but continues to be felt in some degree. It becomes obvious again in woodlands where conditions cause the development of acids, as in beech peat, and may lead to a critical decrease in water-content.

Quantitative study of reactions.—Our exact knowledge of the amount and effect of community reactions is very slight. The investigation of habitat and community by means of instruments is still exceptional. The few quantitative studies so far made have been directed for the most part to other problems, and have rarely dealt with the measurement of reactions. The earliest attempts to measure the reactions of the stages in succession were made in the woodland and prairie formations of Nebraska from 1898 to 1906, and in the mountain and plains formations of Colorado from 1901 to 1910. As already indicated, the first account of the quantitative study of the major reactions of a succession was published in 1910, in connection with the life-history of the secondary sere in burned areas. This was followed by a similar account of the reactions in the grassland stages of the Great Plains (Shantz, 1911). The earlier results in Nebraska and Colorado have as yet been published only in part (Thornber, 1901; Hedgcock, 1902; Clements, 1904; E. S. Clements, 1905; Shantz, 1906).

In addition to the pioneer work of Wiesner (1895, 1904, 1907) upon the reaction on light, a number of measurements have been made during the last decade of habitat factors. While these were not directed at reactions as such, they are often of much value in this connection. Such are the studies of Livingstone (1906) on the relation of desert plants to holard and evaporation, Zederbauer (1907) on the composition of forest light, Yapp (1909) on evap-

oration and temperature in swamps, Dickey (1909), Brown (1910), and Sherff (1913) on evaporation, Knuchel (1914) on quality of forest light, and of a number of others who have investigated bog reactions or evaporation. The first special study of evaporation and succession was made by Transeau (1908) in the study of Long Island vegetation. Dachnowski (1912) has studied the reactions in bog habitats, and Fuller (1911, 1912, 1913, 1914) has investigated the relation of water-content and evaporation to the development of the cottonwood-dune association and the oak-hickory association. Gleason and Gates (1912) have made similar studies of evaporation in various communities in central Illinois. Pool (1914) has recently investigated the water relations of sandhill seres, and Weaver (1914) has studied the relation of evaporation to succession in the Palouse region of Idaho and Washington.

VI. STABILIZATION AND CLIMAX.

Stabilization.—The progressive invasion typical of succession everywhere produces stabilization. The latter is the outcome of greater occupation due to aggregation and migration, and of the resulting control of the habitat by the population. In other words, stabilization is increase of dominance, culminating in a stable climax. It is the mutual and progressive interaction of habitat and community, by which extreme conditions yield to a climatic optimum, and life-forms with the least requirements are replaced by those which make the greatest demands, at least in the aggregate. So universal and characteristic is stabilization that it might well be regarded as a synonym of succession. It has the advantage of suggesting the final adult stage of the development, while succession emphasizes the more striking movement of the stages themselves.

Causes of stabilization.—The essential cause of stabilization is dominance. The latter is partly due to the increasing occupation of a bare area, but is chiefly the result of the life-form. The occupation of annuals in an initial or early stage of a secondary sere is often complete, but the dominance is usually transient. Effective dominance can occur only when the prevailing life-form exerts a significant reaction, which holds the population in a certain stage until the reaction becomes distinctly unfavorable to it, or until the invasion in force of a superior life-form. Dominance is then the ability of the characteristic life-form to produce a reaction sufficient to control the community for a period. Dominance may mean the control of soil factors alone, primarily water-content, of air factors, especially light, or of both water and light. Initial life-forms such as algæ, lichens, and mosses are characteristic but not dominant, since the reaction they produce prevents control rather than gives it. This is the essential difference between the initial and the final stages of succession. While both react upon the habitat, the reaction of the one favors invaders, that of the other precludes them. The reactions of the intermediate stages tend to show both effects. At first the reaction is slight and favors the aggregation of occupants; then it becomes more marked and produces conditions more and more favorable to invasion. On the other hand, when the reaction is distinctly unfavorable to the occupants, the next stage develops with greater rapidity. Each stage is itself a minor process of stabilization, a miniature of the increasing stabilization of the sere itself. Reaction is thus the cause of dominance, as of the loss of dominance. It makes clear the reason why one community develops and dominates for a time, only to be replaced by another, and why a stage able to maintain itself as a climax or subclimax finally appears. Thus, reaction furnishes the explanation of stabilization, as it does of the successive invasions inherent in succession.

Relation to the climax.—The end of the process of stabilization is a climax. Each stage of succession plays some part in reducing the extreme condition in which the sere began. It reacts to produce increasingly better growing conditions, or at least conditions favorable to the growth of a wider range of species. This is equivalent to reducing an excess of water-content or remedy-

ing a lack of it. The consequence is that the effect of stabilization on the habitat is to bring it constantly nearer medium or mesophytic conditions. Exceptions to this occur chiefly in desert regions, though they may occur also in water areas, where processes of deposit and erosion alternate. The effect upon the plant population is corresponding. The vast majority of species are not pioneers, *i. e.*, xerophytes and hydrophytes, but mesophytes with comparatively high but balanced requirements for ecesis. For this reason the number of species and individuals grows larger in each succeeding stage, until the final dominance of light, for example, becomes restrictive. At the same time the life-forms change from those such as lichens or submerged plants with a minimum of aggregate requirements to forms with an increasingly high balanced need. The period of individual development increases as annuals are succeeded by perennials and the latter yield to dominant shrubs and trees. The final outcome in every sere is the culmination in a population most completely fitted to the mesophytic conditions. Such a climax is permanent because of its entire harmony with a stable habitat. It will persist just as long as the climate remains unchanged, always providing that migration does not bring in a new dominant from another region.

Degree of stabilization.—Apart from the temporary stability of each successional stage, the final stabilization of a sere varies greatly in permanence. In the actual seres of the present time this is best illustrated by the water sere in a region where moor and heath appear as stages on the way toward the forest climax. As a consequence of peculiar soil reactions each one is usually a subclimax of unusual duration, and under the artificial conditions evoked by man may persist as an actual climax. A similar effect occurs locally in the Rocky Mountains, where springs keep the soil too moist for the pines which normally succeed aspens on dry slopes. The result is that the aspen remains dominant through a period equal to several stages, and yields only when the final spruce and fir become controlling. This persistence of the aspen is doubtless promoted by repeated fire, which is a universal cause of apparent stability. This is certainly a large factor in the subclimax prairie. Whatever the origin of prairie may have been, its extent and duration are partly due to the effect of fire upon woody communities, followed by a similar influence produced by clearing and cultivation. In all cases of subclimaxes, *i. e.*, of premature stabilization, the activities of man will nearly always prove to be concerned in a large degree.

In the analysis of existing seres it seems evident that complete stabilization occurs only when the climax is controlled by trees, which are the most dominant and hence the highest ecologically of all the life-forms. Developmentally, all other final communities are subclimaxes of greater or less duration; actually, they may exist throughout one or more successional periods. They may owe their existence to any of the following factors: (1) climatic control; (2) reaction upon the soil; (3) interference by man; (4) exclusion by barriers constituted by later dominants. The removal of the check permits complete development and the appearance of the seral climax. The evolution of a new vegetation through long periods of time produces new climax formations and leads to corresponding seres. In the complex successional development of vegetation, since the first appearance of land areas, all possible degrees of stabilization have occurred, with the exception of complete develop-

mental stability. The latter can never occur in vegetation as a whole as long as plants are evolved or conditions changed. Fortunately, our real concern with stabilization is limited to the degree in which it appears in each sere. In other words, it requires study as a developmental phenomenon, and not as a more or less active condition.

LIFE-HISTORY STAGES.

Nature.—While the movement from initial stage to climax or subclimax is practically continuous, there are typically certain periods of comparative or apparent stabilization. These correspond to population or invasion maxima, which mark more or less well-defined stages or communities. As noted elsewhere, such stages usually appear much more distinct than they really are, owing to the fact that the study of succession so far has been little more than the arrangement in probable sequence of stages contemporaneous in different areas. However faint their limits, real stages do exist as a consequence of the fact that each dominant or group of dominants holds its place and gives character to the habitat and community, until effectively replaced by the next dominant. The demarcation of the stages is sharper when the change of population is accompanied by a change of life-form, as from grassland to scrub or forest. In some secondary seres there is little or no change of life-form and the stages are few and indistinct. In rare cases the dominants of the entire sere may be present the first year after a burn, for example, and the well-marked stages are due solely to the rate of growth, which causes the dominants to appear and characterize the area in sequence.

Kinds of stages.—Stages may be distinguished upon various bases. The most obvious distinction is based upon change of population. This is the readiest method, but also the least significant, unless it takes account of dominance as well. Change of life-form is more fundamental and equally convenient, while change of the habitat is even more significant, though much harder to recognize. Dominance, with reaction, includes all of these bases, and is by far the best method. The essential stages are those marked by a dominant or group of dominants. For complete analysis, however, it is desirable to recognize other stages, such as those based upon population and upon effective change of habitat. For general purposes, also, it is convenient to distinguish stages with reference to their position in the course of development. As a consequence, the best method of treatment is to base stages upon successive dominants and to recognize substages whenever a change of character makes it desirable or necessary. This is usually in the early part of seres, before dominance is clearly established. At the same time it is helpful to group stages for reference or to bring out certain relations. They may be grouped into initial, medial, or final, or into temporary or migratory, on the one hand, and permanent, stable, ultimate, or climax on the other. As to habitat, one primary sere, for example, may show rock, gravel, grassland, and woodland stages, and another water, sedgeland, grassland, and woodland. The corresponding life-form stages would be lichen, moss, herb, grass, scrub, forest, and algæ, herb, sedge, grass, scrub, forest.

Rôle of life-forms.—Since dominance and reaction are consequences of the life-form, it follows that the main stages in development are marked by

different life-forms. The latter is used in a broader sense than is usual; it includes not only the vegetation form, with its synonyms, biological forms, growth-forms, etc., but also the habitat forms, and something of the reproduction form as well. The life-form, in short, comprises all of the structures which mark the species as an ecological agent. Its fundamental correspondence with the habitat is obvious. The forms of the aërial shoot are of the first importance, but the organs of perennation have to do directly with occupation and with ecesis. The root-forms are usually of secondary importance, though in sand and gravel in particular they play a conspicuous rôle. In essence, the life-form is the superposition of water and light adaptations upon the vegetation form, though in cryptogams especially, the latter corresponds closely to the reproduction or taxonomic form.

It is difficult to refrain from speaking of life-forms as lower and higher with respect to their position in succession. This is determined by their demands upon the habitat as well as by their reaction. In the case of the pioneers of most primary seres this is warranted by the taxonomic development as well, and there can be little objection to this as a convenient comparison. Because of their universal presence, the plankton algæ of water-bodies are hardly to be regarded as pioneers in a particular water sere, though this is their position in the geosere. The actual pioneers of a water sere are charads, submerged mosses and flowering plants, with a life-form characteristic of the habitat. Probably submerged attached algæ belong here also. Floating forms, primarily phanerogams, mark the first division of the habitat into two media, water and air, and serve as a natural transition to the reed form. In this there is a complete differentiation by the two media into aërial shoot and aquatic roots and shoot. In many cases it is desirable to distinguish the sedge form from the reed, though there is manifestly no sharp line between them. This is true of the grass form in some measure, but it is clear that the habitat has changed materially as a rule. The change from grassland to woodland is the most significant, since the persistence of the stems greatly emphasizes the reaction upon light and other air factors. While the woody form is consequently sharply distinguished, this is not always true of the subordinate forms, bushes, shrubs, and trees, since the difference is primarily one of size. In spite of its aërial position, *Sphagnum* is essentially a submerged moss. In many cases it is clearly a pioneer life-form, though its ability to bring about the swamping of vegetation complicates its treatment. The shrubs characteristic of heath belong to a peculiar habitat modification of the shrub form, produced directly or indirectly by acid soil, by deficient aëration or by winter.

In rock seres, the pioneer life-form is the alga, when the rocks are wet, and the lichen when they are dry. It is interesting, if not significant in this connection, that the alga is an essential part of the lichen pioneer. In fact, it seems probable that algæ, especially *Pleurococcus,* may become established on exposed rocks during wet periods and thus actually precede the lichens. Such must be the case with rock lichens in which the spores are still efficient. On moist rocks, algæ may also be followed by lichens, especially Collemaceae, though the algal character of moss protonema enables the mosses to appear quickly, and often, it would seem, must permit them to be the first pioneers. On dry rocks there is a fairly distinct successional difference between the

crustose and foliose lichen forms. The moss form, with its minute rhizoids and power of withstanding desiccation, quickly follows the lichen stages and may even precede the foliose lichens. The pioneer herb form on exposed rock has the mat habit as a rule and resembles the moss cushion in many respects. It is quite different in character from the forms of herb and grass which grow in the rock clefts. These belong essentially to the next stage, as they actually grow in soil and are only apparent rock plants. With the appearance of grasses and herbs, the later life-forms of the rock sere become the same as in the water sere.

The sequence of life-forms in secondary seres is essentially the same as in primary ones. A characteristic exception, however, is furnished by the fact that the pioneer life-forms are perhaps never the same. The approach is sometimes very close, as, for example, when mosses appear after a burn. In practically all such cases flowering plants develop the same year, and the mosses, as well as possible algæ and lichens, never form a characteristic stage which persists for several or many years. In fact, the very nature of secondary succession as a course of development less complete than the primary one precludes its beginning with the original initial stage.

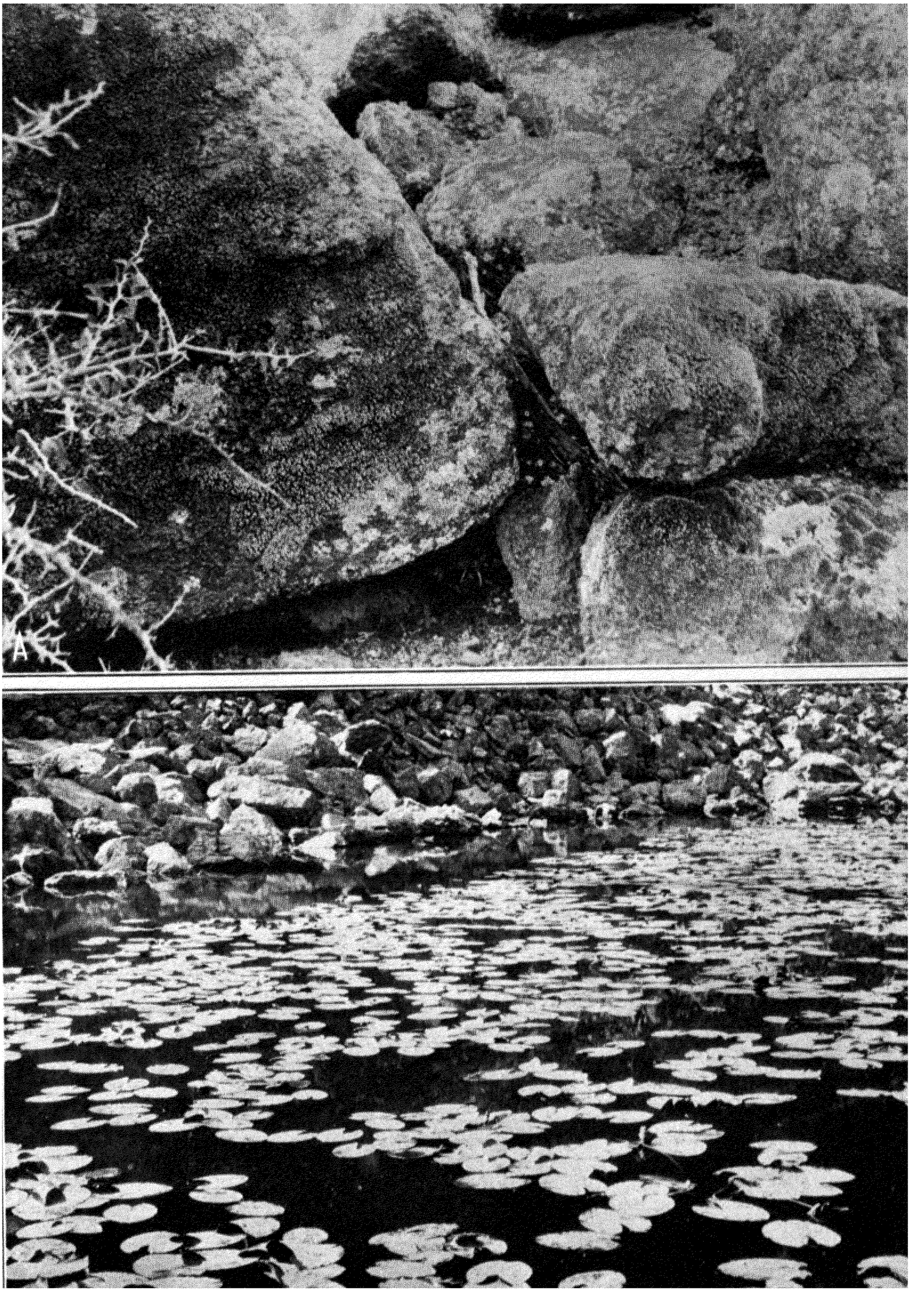
Reasons why plants disappear.—Stages are obviously the result of the disappearance of occupants and the appearance of invaders. The causes of the disappearance of plants are thus in large part the explanation of the stages themselves. Most species disappear wholly, though some persist through more than one stage, usually in this case becoming subordinate. Others are reduced to a small or insignificant number of individuals, which may persist as relicts for a long time. Plants disappear for one or more of the following reasons: (1) unfavorable conditions due to reaction; (2) competition; (3) unfavorable conditions or actual destruction due to parasites, animals, or man; (4) old age. The first two are the universal causes of disappearance, and while reaction is much the most important, its effect is distinguished with difficulty from that of competition. Complete, or nearly complete, destruction of a community results in secondary succession. It is only when the destruction operates upon the dominant or dominants alone that a change of stage may occur without clearly producing a secondary sere. This may occur in the selective lumbering of a mixed forest, and in grazing when not too close, but there is a question in both cases whether this is not really imperfect secondary succession. The influence of old age in the disappearance of dominants is far from evident. It seems important in deciding the competition between short-lived trees, such as aspens and birch, and long-lived conifers, and in the resulting dominance of the latter. But it is quite possible that this is really due to differences in growth and especially in height. In the case of pioneers with radial growth, such as lichens, cushion herbs, and grass, the death of the central portions seems due to what may well be called old age. This process sometimes extends throughout the whole mat, and is apparently a factor of some importance in the disappearance of the mat pioneers of alpine gravel-slides, as in that of rock lichens.

Reasons why plants appear at certain stages.—Migrules are carried into an area more or less continually during the course of its development. This is doubtless true of permobile seeds, such as those of the aspen. As a rule,

however, species reach the area concerned at different times, the time of appearance depending chiefly upon mobility and distance. As a consequence, migration determines in some degree when certain stages will appear. The real control, however, is exerted by the factors of the habitat, since these govern ecesis and hence the degree of occupation. The habitat determines the character of the initial stage by its selective action in the ecesis of the migrules. In all secondary areas, however, it must be recognized that the conditions of the habitat are largely due to the reactions of the original vegetation. After the initial stage the development of succeeding ones is predominantly, if not wholly, a matter of reaction, more or less affected by competition. In addition, some stages owe their presence to the fact that certain species develop more rapidly and become characteristic or dominant, while others which entered at the same time are growing slowly. This is a frequent explanation of stages of annuals, as also of stages of perennials preceding scrub or forest in secondary succession.

Reasons why plants appear before their proper time.—The appearance of a species before its usual place in the sequence is generally due to migration in such amount that the handicap of more or less unfavorable conditions is overcome. It is most frequent in secondary seres, where the factors are less extreme, and the majority of the species can become dominant as soon as a sufficient number of migrules appear. In primary succession, especially, species can become characteristic only after the reactions have reached a certain point. In the great majority of cases where a species appears out of order, it is due to local variations in the area. The premature development of an entire stage is caused by agencies which suddenly or rapidly change the habitat in the direction of the reaction. This is particularly true of areas which are affected in this way by animals or man. The number of stages omitted will depend upon the rate and degree of change. It is not unusual for this telescoping effect to eliminate two or more stages. The agencies which accelerate reaction may also retard it, so that stages may be delayed by the undue persistence of an earlier one. In all secondary successions the time of appearance of shrub and tree stages depends in the first degree upon the action of the denuding agent. When this destroys all seeds and propagules, the sequence of stages will be determined as usual by the mobility of migrules and by the habitat. When seeds or living parts of dominants escape destruction, the species concerned will take possession at once, or as soon as their development permits. Thus when an aspen forest is burned the root-sprouts often make the aspen again dominant the following season, and succession is found only in the renewal of the undergrowth. As noted in other connections, the seeds of lodgepole pine and similar pines are available in large numbers after fire, with the result that lodgepole pine reappears the first season, though its slow growth to dominance permits the rapid development of several stages. A similar effect has been noted by Hofmann in the forests of the Pacific slope when burned. The seeds of various species lie dormant for several years at such a depth in the forest duff or soil that they escape the fire and are ready for germination the year following.

Initial stages.—No sharp line exists between initial and medial stages. The distinction, though convenient, can be only relative. Seres vary greatly in the number of stages and especially in the number and character of initial



A. Initial stages of a xerosere, lichens, mosses, and liverworts, Picture Rocks, Tucson, Arizona.

B. Initial stage of a hydrosere, *Nymphaea polysepala*, in Two Ocean Lake, Yellowstone Park.

development at the floating, the reed, or the sedge stage, just as rock may disintegrate without the presence of lichen or moss stages, and the succession begin with the development of herbs or grasses.

Of all the initial stages, the first is in many ways the most significant. In consequence, it seems desirable to distinguish it as the *pioneer* stage. This term is most applicable to the extreme conditions of a primary area, though two kinds of pioneer stages may well be distinguished, as already suggested. Lichens, on the one hand, and submerged plants on the other, are the usual pioneers for rock and water seres respectively. For the present it seems best to designate only the first initial associes of the primary sere as the pioneer stage, and to leave the further distinction between actual and normal pioneer stages for future needs. The case of the first stage of secondary seres is different, however. The initial conditions are rarely extreme and the invasion is correspondingly extensive and rapid. The invaders do not meet pioneer conditions in the sense of primary areas, and the first stage is very short, often lasting but a year or so. The degree of occupation is usually high and the number of stages so few that only the first one can be regarded as initial. As a consequence it seems desirable to speak of a pioneer stage only in primary succession and to designate the opening stage of a secondary sere as the first or initial stage.

Medial stages.—The general demarcation of these from initial stages has been sufficiently indicated above. They are characterized by a fairly uniform density, by well-developed dominance, and usually by the increasing abundance of humus, together with medium amounts of water. They consist of well-developed communities in which layers have begun to appear. The most characteristic life-forms are grasses and shrubs. Medial stages may best be regarded as including all the stages between initial and climax ones. In all seres but those with a forest climax, these are all the stages after the initial ones but the last. When succession ends in forest, it seems desirable to consider all the successive forest communities as climax stages, though only the last is the climax association. The number of medial stages is several in primary seres, and few, often only one or two, in secondary ones. In both, the term must be regarded as comparative and relating chiefly or solely to position in the sequence, since grassland stages are medial in a region with a forest climax, and climax in a region of climatic prairie.

THE CLIMAX.

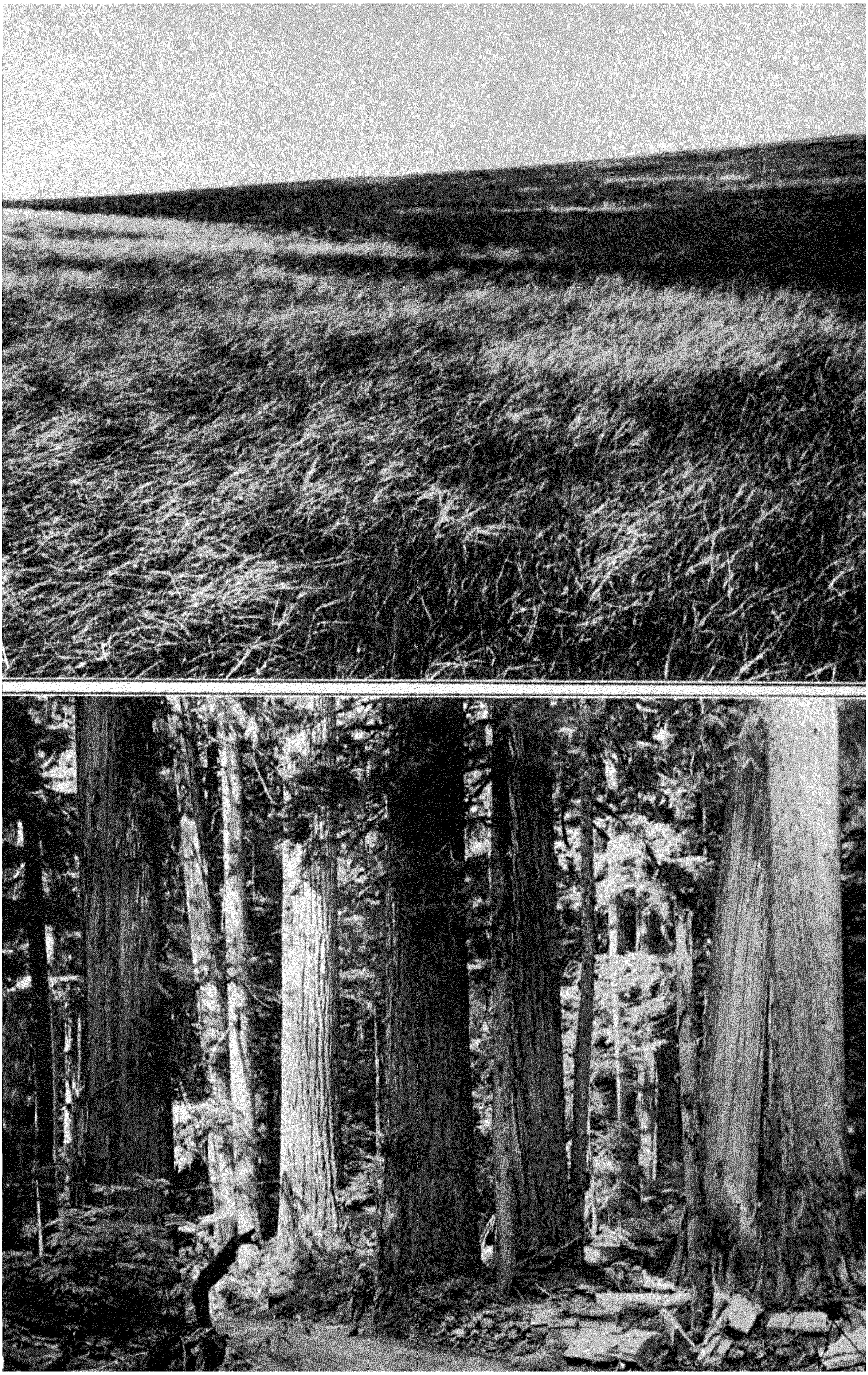
Concept.—Every complete sere ends in a climax. This point is reached when the occupation and reaction of a dominant are such as to exclude the invasion of another dominant. It does not prevent the entrance of subordinates, and it is conceivable that a codominant might enter also, though no case of this is known. The climax marks the close of the general development, but its recognition is possible only by a careful scrutiny of the whole process. Duration is in no wise a guide, since even pioneer stages may persist for long periods, and medial stages often simulate a climax. The test of development is especially necessary in climax stages, *i. e.*, those in which the dominants belong to the same life-forms as the climax dominant. It is not merely indispensable to trace and retrace the course of succession in a particular

locality. It is also imperative to follow the development in all parts of the climatic region where dominants occur which are similar to the one supposed to be the climax. There is no field in ecology where it is so necessary to employ both intensive and extensive methods to secure permanent results. The reason for this is obvious when it is fully recognized that the climax formation is the clue to all development and structure in vegetation.

Nature.—The fundamental nature of the climax and its significance in the life-history of a vegetation are indicated by the fact that it is the mature or adult stage of the latter. As stated elsewhere, the climax formation is the fully developed community, of which all initial and medial communities are but stages of development. The general behavior of the formation as a complex organism resembles very closely that of the simple organism, the individual. The recognition of the latter is so natural and necessary a prelude to the study of its development and organization that it is taken for granted. In like manner the recognition and limitation of climax formations is indispensable to a proper developmental study of vegetation. It is not at all the usual method of approach as yet, because its unique importance has not been generally recognized, but in the future much more attention must be paid to the climax stage if the problems of development and structure are to be clearly foreseen and solved. In fact, the study of succession in any climatic region should be begun by an intensive and extensive study of the adult organism, the development of which is to be traced. This is especially necessary in view of the complex nature of succession and the number of adseres and subseres that may occur in the development of any formation. The need of such a method of study is further emphasized by the fact that prisere and subsere are but reproduction processes of the formation and as such can be understood only by an understanding of the formation itself (plate 13, A, B).

Relation to succession.—The explanation of the universal occurrence of a climax in succession lies in the fact that the succession is reproduction. The reproductive process can no more fail to terminate in the adult form in vegetation than it can in the case of an individual plant. In both instances it may fail under abnormal, *i. e.*, unfavorable, conditions. The lack of light in dense thicket or woodland will prevent the maturing of herb or woody plant, as it will of aquatic and amphibious plants when too deeply submerged. An excess of water will have similar effects, while a deficit often suppresses the vegetative stages in large degree. The action of man or animals may keep the plant in an immature condition throughout its life history. While the response is usually more complex, the behavior of the formation is strictly comparable. Natural or artificial factors may hold it almost indefinitely in an imperfect condition of development, *i. e.*, in practically any initial or medial stage, or may cause reproduction of little more than the adult stage alone. Man in particular may cause a developmental stage to become permanent, or to recur so constantly that it appears to be fixed.

The underlying causes of complete development of the formation are to be sought in the habitat, just as they are in the case of the individual. Favorable or normal water and light relations result in normal or complete development; unfavorable or abnormal conditions cause suppression of part of the course. The significant difference lies in the fact that the reactions of the individuals



A. Climax prairie of *Stipa* and *Agropyrum*, Winner, South Dakota.
B. Climax forest of *Pseudotsuga*, *Tsuga*, and *Thuja*, Mount Rainier, Washington.

as a community produce a cumulative amelioration of the habitat, a progressive improvement of the extreme, intrinsic to the continuance of development itself. In the case of heath, the production of "bleisand" and "ortstein" are unfavorable to further development, but such a consequence of reaction is wholly exceptional. Indeed, this hardly constitutes an exception, since the persistence of such conditions produces a climax. The climax is thus a product of reaction operating within the limits of the climatic factors of the region concerned. The latter determine the dominants that can be present in the region, and the reaction decides the relative sequence of these and the selection of one or more as the final dominant, that is, as the adult organism.

Kinds of climaxes.—The climatic formation is the real climax of the successional development. As has been seen, various agents may interpose to prevent complete development. The result is to produce apparent climaxes of greater or less duration. These depend absolutely upon the continuation or recurrence of the action which inhibits further development. They disappear as soon as the causative force is withdrawn, and the course of succession resumed in consequence. Such apparent climaxes are always subordinate to the normal developmental or climatic climax, and may accordingly be distinguished as subclimaxes. The application of this term is based upon the two-fold meaning of the prefix *sub,* of which the original sense is *beneath* or *under,* and the transferred meaning *somewhat* or *rather.* The subclimax is always below or before the climax proper in point of time, and actually beneath it in such coseres as those of peat bogs. Likewise it is subordinate developmentally, though in dominance and persistence it may resemble a true climax very closely. In addition to subclimaxes, which are constituted by some stage antecedent to the climatic formation, there may be distinguished potential climaxes which are often subsequent. A potential climax is the actual climax of an adjacent region. It is called potential because it will replace the climax of the region concerned whenever its climate is changed. The potential climax of plains grassland is scrub if the rainfall is increased; it is desert if the temperature is increased. As is later shown at length, potential climaxes stand in a zonal relation to a particular formation, and this relation is that of the sequence of successional stages.

Subclimaxes.—Various causes produce subclimaxes. Such are (1) soil, (2) reaction, (3) competition, (4) migration barriers, and (5) man. In spite of the greatest difference in their action, they agree in preventing development by handicapping or destroying some stage, usually a climax one. Apart from plant reactions, such an influence is probably exerted by the soil only when it contains an excess of salt. In the Great Basin the climatic formation is that of the sagebrush (*Artemisia tridentata*), but vast alkaline stretches will long be covered by *Sarcobatus* and *Atriplex.* As a consequence of their reaction these will yield theoretically to *Artemisia* in the course of time, and this seems to be actually taking place at the margins of the alkaline area. In the present state of our knowledge, however, it is impossible to be certain that this can ever occur in the heart of the region without a change of climate. Reactions which retard succession instead of promoting it are few, but they are of great importance. There seem to be but two of these, that of *Sphagnum* in accumulating water, and that of moor and heath in producing acids or other harmful substances. These reactions, together with the consequent pro-

duction of heath-sand and "orstein," appear to enable moor and heath to persist for a long time over vast areas. There is, however, some warrant for thinking that these subclimaxes are due wholly or partly to the action of man.

The exact rôle of competition is more difficult to ascertain, but there can be little doubt that it is important and sometimes controlling in maintaining a grassland subclimax. This is said to be true of the Ceylon patanas by Pearson, and it is also confirmed by evidence from the prairies and from mountain meadows. A subclimax due to barriers to immigration occurs whenever such final dominants as *Picea* or *Fagus* are prevented from spreading throughout a natural region. Thus *Pinus* and *Quercus* have formed or still form subclimaxes in areas ultimately to be occupied by beech or spruce. In the valleys of the Missouri River and its tributaries in Nebraska, as elsewhere along the western margin of the Mississippi Basin, the forest is in a subclimax stage composed of *Quercus, Hicoria,* and *Juglans.* Further westward, the valley woodland is a subclimax formed by a still earlier stage composed of *Populus* and *Salix.*

Subclimaxes due wholly or partly to the activities of man are numerous. Conspicuous causes are burning, clearing, and grazing. These produce subclimaxes in a particular area by disturbance and destruction of the community. This results in subclimaxes in adjacent areas in consequence of destruction of the source of migrules. Grassland areas are produced the world over as a result of burning and grazing combined, and they persist just as long as burning recurs. Woodland is frequently reduced to scrub by fire, and the scrub often persists wherever repeated fires occur. Even when fires cease with the settlement of a region, grassland and scrub subclimaxes persist for a long time because of the more or less complete removal of the forest. The clearing of the forest in connection with lumbering or cultivation may result in more or less permanent scrub. When clearing is followed by fire or grazing or by both, as is often the case, the scrub may be entirely replaced by grassland, which remains as a subclimax as long as the causes are effective, or may persist almost indefinitely in consequence of the removal of natural forest and scrub from the region. In the case of silvicultural activities, it is evident that any forest stage may be fixed as a subclimax, or that a new subclimax may be produced artificially by the planting of exotics. Similar modifications are possible in the treatment of natural grassland. The final climax in a grassland region, such as that of the Great Plains, may be inhibited by fire or grazing. The area may remain for a long time in a grass subclimax, such as the *Aristida* consocies, or it may show an undershrub climax of *Gutierrezia* and *Artemisia.*

Potential climaxes.—As has been stated previously, zones of vegetation indicate the changes of vegetation possible in consequence of a change of climate. This is fairly evident in the case of zones which correspond to marked differences in latitude or altitude, but it is equally true of other great zones, such as the prairie, plains, and interior basin of North America. These are all responses of vegetation to a progressive change in the controlling factors, as is true of the more striking zonation of ponds, streams, islands, etc. The regional zones are produced by the cumulative change of climatic factors in one direction, while the local zones are due to the gradual change of water-content, often in consequence of reaction. The latter are independent of climate to the extent that they exist beside each other, but they are only

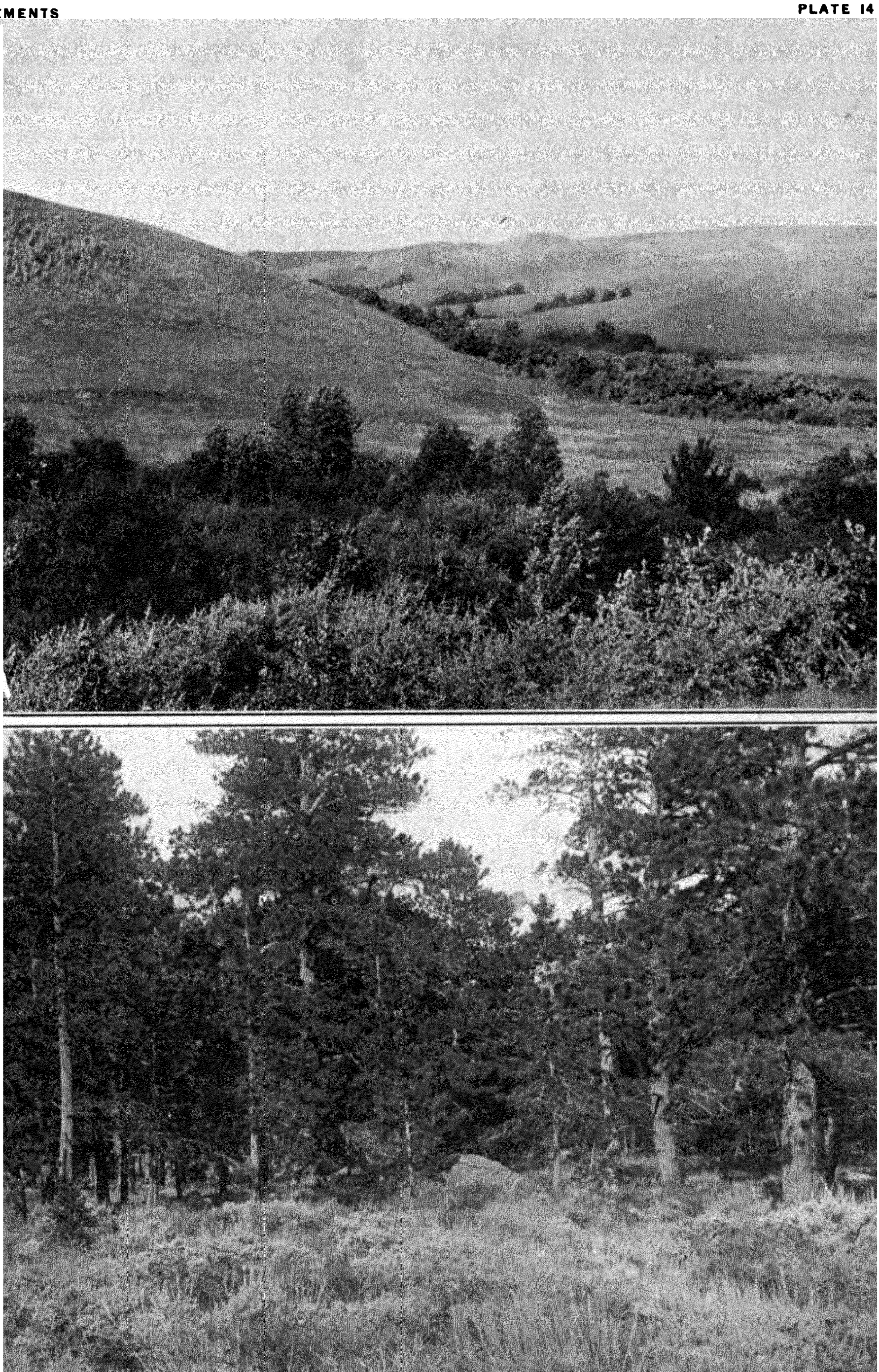
records of a development which comes increasingly under climatic control with every step away from the original extreme of soil conditions. The zones of a prairie lake are the result of the reaction control, or what might be called the habitat control, of succession, but the paramount part of climate in the development is shown not merely by its setting the usual climax limit, but by the fact that it can fix an earlier or later limit. Normally, the stages of invasion end with the outermost zone, since this is the climax in which the new area for development has been set, but a change of climate in the direction of greater rainfall or less evaporation would continue the development beyond prairie into woodland. The latter then becomes an intrinsic member of the successional sequence as recorded in the series of zones.

Changes of climate.—A change of climate can not initiate succession except where extreme drouth or frost destroys essentially an entire plant community. Practically no such instances are recorded for native vegetation, and such climatic changes as we know can only continue a sere already begun or bring it to a close in a stage earlier than the climax. Indirectly, changes of climate may result in new areas being produced by other agencies as a consequence of increased rainfall. When operating over long periods, they may produce profound changes of the flora, and hence alter the whole climax community and its development. The effect of climatic oscillations may be seen from year to year in the ecotone between two climatic associations. In short, the ecotone is largely a record of the effects of small variations of climate. If accumulated or allowed to act in one direction, the latter are sufficient to give the advantage to one of the contiguous associations. In the midst of the prairie region, the forest edge of the valleys yields in years of severe drouth, as in 1893-1895, while in a series of years with unusual rainfall it advances visibly. If similar dry or wet conditions become permanent, the forest would gradually give way before the prairie, or the latter would disappear before the forest. The completeness of the replacement would depend upon the amplitude and the duration of the climatic change. All timberlines, especially alpine ones, show similar movements, and the latter can be recognized in all herbaceous ecotones, though with less readiness. When the change of climate favors mesophytic conditions, the existing seres are continued by the addition of one or more stages dominated by higher life-forms. In the case of the prairie, the potential climaxes in this case are deciduous forest in the east, and scrub and pine woodland in the west. An efficient increase in rainfall might well bring these two together, and result in the prairie climax being replaced by a pine climax in the present plains area and a deciduous forest climax in the prairie area proper. It is far from improbable that something of the sort has happened in the past. Such a contact has actually occurred in the valley of the Niobrara, where *Pinus ponderosa* reaches its eastern limit just east of the one hundredth meridian, where it is met by *Juglans, Ulmus, Tilia,* and other members of the deciduous woodland (Bessey, 1887, 1896:109, Pound and Clements, 1900:322). If the swing of climate results in decreased rainfall, the potential climax is found in the areas with a vegetation one stage more xerophytic than the existing climax. These are the crests and ridges on which the present climax has not yet established itself, or the secondary disturbed areas which are in the subclimax stage. The corresponding communities of *Aristida,* or of *Gutierrezia-Artemisia,* would probably become the climax vegetation, though

certainty is impossible since the present tendency over much of the prairie and plains area is favorable to scrub and woodland.

Preclimax and postclimax.—The significance of potential climaxes is best seen in the case of mountain ranges which rise directly from the plains. Such are the Front and Rampart Ranges of Colorado. In these, the narrow zones stand out sharply, and the effect of possible changes of climate is demonstrated most clearly by east-and-west cañons. On the north exposure of these a mesophytic association may descend far below its horizontal limit and thus occur alongside of one which it would eventually replace if the rainfall were to increase generally. On south exposures of the cañon, the more xerophytic communities ascend far above their usual limit, and place themselves in contact with the normal climax which would yield to them in case of decreased rainfall. As a consequence it becomes possible to recognize two kinds of potential climaxes. The one indicates what will happen if a change of climate results in increased water-content, thus emphasizing the normal reaction in the sere. It continues the development by replacing the climax and it may be termed the postclimax (Gr. πος; Lat. *post,* after). The other foreshadows the climatic change which reduces the water-content, and thus sets a lower limit to the increase of the holard by reaction. As a consequence, development would cease before reaching the climax proper, and the potential community, which would now become the actual climax, may be called the preclimax (Gr. πρι; Lat. *prae,* before). Thus, every climax area or formation is in contact with one or more climax areas which bear the relation of preclimax and postclimax to it, and are in a more or less complete zonal series with it. Subclimaxes are practically always preclimaxes (plate 14, A, B).

Changes of climax.—As already noted, the climax may change in consequence of a single efficient variation of climate or of the development of an essentially new flora as the outcome of long-continued evolution due to climate. In addition, the climate may show a cumulative change, or it may exhibit great alternations, such as those indicated in Blytt's theory (1876). Both of these phenomena were associated, it would seem, with the glacial period. It is not difficult to surmise the behavior of the successive climax formations in the face of the oncoming ice. A gradual invasion must have produced preclimaxes in all of the seres actually in development, before it overwhelmed each climax area. The area just south of the final limit must have developed a series of preclimaxes, ending in arctic tundra. Each recession of the ice must have changed seral climaxes into postclimaxes, and each new advance would cause the existing seres to terminate in preclimaxes. The final withdrawal of the ice would give new areas for colonization by an arctic flora, and hence a new arctic climax, while the original arctic climax about the southern edge would yield to the postclimax of heath or aspens and conifers just south of it. In a similar manner, the postclimax of deciduous forest would replace the conifers, and these again a new arctic climax of which they were the potential climax. Finally, when climatic equilibrium was established, the arctic zone south of the original ice would have had three or four successive climaxes, and the number of climaxes would decrease by one for each zone to the northward. For any particular period, each climax zone may have had a sequence of seres, *i. e.,* a cosere, all ending in the actual climax. In the case of the alternating wet and dry climates which followed the glacial period, the postglacial



A. Postclimaxes of scrub (*Shepherdia*, *Amelanchier*, etc.) and of woodland (*Ulmus*, *Fraxinus*, *Quercus macrocarpa*) in prairie climax, Gasman Coulée, Minot, N. D.

B. Sagebrush preclimax (*Artemisia tridentata*) and *Pinus ponderosa* climax, Estes Park, Colorado.

deposits seem to furnish convincing evidence of a sequence of climaxes derived from postclimaxes. Thus, the arctic climax, the *Dryas* association, was succeeded by an aspen climax, the latter by a pine climax, this by an oak climax, and the oak by the beech climax of to-day. The sequence apparently corresponds with the gradual amelioration of temperature in large degree, and is concerned with changes of rainfall only in so far as they favored or hindered the growth of *Sphagnum,* and thus caused successive seres, the climaxes of which were preserved by being embedded in the peat-bog.

VII. STRUCTURE AND UNITS OF VEGETATION.

DEVELOPMENT AND STRUCTURE.

Relation.—Development is the process by which structures are fashioned. This is as true of the climax formation as it is of the mature individual. Each is a climax stage with characteristic structure produced by development. Moreover, both formation and plant exhibit structures in the course of growth. Some of these are retained and contribute to the final form, others are transient and disappear completely after they have fulfilled their function. In the case of the individual, most of the structures persist and play their part in the work of the adult. That this is not necessarily true is shown by the usual behavior of cotyledons and stipules. It is also seen in the complete or partial disappearance of leaves and stems, and especially in the fate of flower parts. From the nature of the plant community, the earlier structures are replaced by later ones, though they may persist in some measure, especially in secondary seres. Finally, the development of both formation and plant is a series of responses to the progressive change of basic factors, which not only control the course of development but determine also its culmination in the adult.

Kinds of structure.—The nature of succession as a sequence of communities from extreme to medium conditions determines that its major and universal expression in structure will be zonation. This is convincingly shown in water seres, where the zonation from the center to the margin, due to water relations, is repeated in the zones or layers which succeed each other as the center is shallowed. In essence, the zones of the margin move successively over the surface, and are recorded as superimposed zones in the peat. Whenever conditions change abruptly instead of gradually, zonation is replaced or obscured by alternation. The latter is strikingly evident in extensive communities which are disturbed here and there by denuding agents. The resulting bare areas give rise to secondary seres, the stages of which when viewed as static communities seem to be unrelated to the circumjacent vegetation. As a matter of fact, they are merely incomplete expressions of successional zones, as is readily observed when the denuding force has operated unevenly over the entire area. The layers of forest and grassland are zonal structures which are more or less evidently connected with succession. The seasonal aspects of vegetation, though recurrent, are also developmental, and often stand in intimate relation to layering.

Zonation.—Zonation is the epitome of succession. Zones are due to the gradual increase or decrease in a basic factor, typically water, from an area of deficiency or excess. Successional stages are produced by the slow change of a bare area from one of deficiency, *e. g.*, rock, or one of excess, water, to more or less medium conditions. In the case of water, for example, the bare area of excess is the starting point for the series of zones, as it is for the series of stages. In short, zones are stages. This fact has been generally understood in the case of zones around water bodies, in connection with which it was first clearly stated by De Luc (1810:140) in the following sentence:

"The succession of the different zones, from the border of the water towards the original border of sand, represents the succession of changes that have taken place through time in each of the anterior zones, so that in proportion as the reeds advance, new zones are forming behind the advancing reeds on the same places which they thus abandon."

It has not been recognized that it reveals a basic and a universal principle. It is just as true of the climax formations of a continent, with zonal disposition in accordance with latitude and altitude, as it is of the zones of a lake or river or those of hill or ridge. The latter are zones of actual succession, the stages of existing seres; the former are zones of potential succession, and indicate the further stage of development in the event of a change of climate. Both are possible stages of the same great development, and are equally controlled by the gradual change of conditions, though the change in one case is climatic, in the other edaphic.

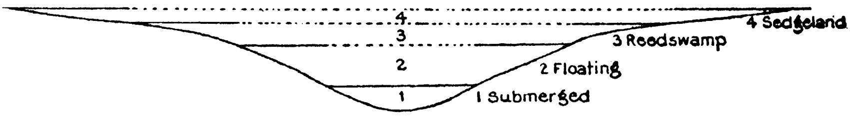


Fig. 3.—Schematic representation of the development of the hydrosere, showing identity of zones and seral stages. Straight lines indicate zones, and dotted ones their extension across the pond as the latter is shallowed.

The intrinsic relation between zones and stages is best proved by the zonation about water, on account of the relatively rapid decrease in water-content. It is equally well shown by areas with rapid increase about a dry center, such as islets in the lakes of arid regions, but these are relatively infrequent. Ponds and streams with gently sloping margins often show at one time a complete series of zones representing the successive stages of development to the climax association. The relation of these zones in time is clearly demonstrated by projecting them across the water center, as is seen in figure 3. Such a projection occurs by degrees during the course of development, until the center is occupied in the proper sequence by every stage from the submerged to the climax community. The proof of this is found in practically all peat deposits, but especially in those where the development has been gradual and complete. The actual extension of the various zones over the water-body or a portion of it occurs when a pioneer or subpioneer community, such as a *Sphagnetum*, develops as a floating mat which becomes anchored at the bottom or the side. Such seres furnish the complete demonstration of the identity of zones and stages, and also serve to emphasize the fact that every zone has a temporal as well as a spatial relation, and hence is the result of development.

The filling by reaction of a pond or lake with a uniformly shallow bottom and abrupt banks is of especial significance in correlating climatic zones with edaphic ones. In such ponds, which are typical of the prairie region, the spatial relation is over-emphasized, the temporal relation obscured. It not infrequently happens that there is complete unconformity between the pond community and the climax vegetation in which it occurs. In a word, the usual zones are lacking, since there is no gradual shallowing of the water toward the climax area. The consequence is that each stage, instead of form-

ing a zone as normally, occupies the whole area for a longer or shorter period in the usual sequence of succession. It shows no organic connection with the climax association until the development is completed, and in itself furnishes no direct evidence of succession. In fact, when the area occupied by such a community is large, it simulates a climax association. Apart from its resemblance to other communities whose development is known, its real nature can be ascertained only by actually following the sequence of stages or by probing the deposits of plant remains. As a matter of fact, water seres are too well understood to cause difficulty in this connection, and the illustration is of importance only because it clarifies the developmental relation of the great climatic zones. The latter also seem to have no successional connection, but this is only a seeming, as has already been indicated under potential climaxes. An effective swing of climate at once places each climax area in successional articulation with an adjoining one, and reveals its essential nature as a developmental zone. It has been shown above that the climax changes of the glacial and the postglacial periods not only transformed climax zones into successional stages, and the reverse, but also that it left a record of such zonal stages in the layers of peat-bogs.

The zonation of hills and ridges in the prairie formation is typical of the relation between structure and development. Owing to the more or less uniform nature of grassland, distinct zones are rarely evident, but a careful scrutiny shows that a majority of the societies are in zonal relation. Exposed rocky crests bear lichen colonies, about which are xerophytic communities of *Lomatium, Comandra, Meriolix,* and others. Middle slopes are occupied by more mesophytic species, such as *Astragalus, Erigeron, Psoralea,* etc., and the bases and ravines by meadow species, especially grasses and sedges. In some of the ravines small marshes or ponds develop and add one or more zones to the series, while in others, thickets of *Salix, Rhus,* or *Symphoricarpus* appear, making possible the invasion of woodland herbs, and the occasional entrance of *Populus* or *Fraxinus.* Imperfect as the zonation of the prairie is, it furnishes an indubitable record of the development of the association from xerophytic ridge communities on the one hand and from ravine communities of meadow and marsh on the other. In addition, the ravine thickets suggest the fate of the prairies when confronted by an increase of rainfall, or when artificial barriers to the spread of woodland are withdrawn.

The zonation of fringing forests is perhaps best seen in prairie and plains regions, owing to the fact that the decrease of water-content from the edge of the stream to the dry grassland takes place rapidly. In addition, there is a similar rapid decrease of humus and increase of light intensity. In many places actual zones are lacking or fragmentary, owing to local conditions; in others, the complete series may find expression. In the Otowanie Woods near Lincoln, *Salix, Populus,* and *Ulmus* either indicate or constitute narrow zones from the water to the oak-hickory climax. In the direction of the grassland, *Fraxinus, Rhus,* and *Symphoricarpus* constitute as many zones in more level areas, while on steep slopes only a narrow band of thicket may occur, or the scrub oak (*Quercus macrocarpa*) may gradually dwindle into a shrub but a foot or two high.

Relations of climax zones.—Like all zones, climatic ones are due to a gradual change in the amount of one or more controlling factors. They differ

from edaphic zones in the fact that the plant reactions affect the general climate but little. They are in consequence relatively permanent, and disclose their successional relationship only as a result of pronounced climatic changes. The zonal arrangement of climax associations and their consociations is produced by the gradual decrease in water and temperature from an area of excess. The effect of reduced temperature is found in the direction of the poles, and produces east and west zones. The effect of diminishing rainfall operates from coast to interior, and is recorded in zones which run north and south. The two are necessarily superimposed, and the final expression in terms of structure is further complicated by the influence of mountain ranges and large interior bodies of water, such as the Great Lakes. Mountain ranges may not only disturb the primary climatic zones, but they also present new regions of relative deficiency and excess, and consequent zonation.

Direct evidence of the successional relation of climax zones, such as is universal for edaphic zones, is not abundant. There are, however, several sources of conclusive proof of their essential developmental connection. The most important evidence is that furnished by peat-bogs and tufa deposits, which bear witness to successive climax stages due to change of climate. The similarity of these to zoned climax communities of to-day leaves no doubt of their zonation, which is also attested by the fact that the zones of to-day about water-bodies are recorded in superimposed layers of plant remains. Further evidence is afforded by the vegetation of cañons. The well-known fact that the local climate of the north and south exposures is very different has already been dwelt upon. The result of this difference is to produce in miniature the effect which a general climatic change would cause over the whole mountain-slope. A change in the direction of greater heat or dryness would tend toward the xerophytic preclimax of the south exposure, while the opposite change would give rise to the postclimax of north exposures. Indeed, the behavior of such consocies as that of *Pinus ponderosa* is direct proof of the developmental nature of climax zones. At lower altitudes it forms a xerophytic climax over a vast stretch of the Rocky Mountain region; at elevations 2,000 to 3,000 feet higher it is the subfinal stage in the development of spruce forest. In other words, its spatial or zonal relation as a mountain climax to the subalpine spruce climax indicates its precise successional relation in the development of the latter.

The bilateral zones of river valleys also furnish evidence of the potential development consequent upon climatic change. This is especially true where the valley lies in the direction of decreasing rainfall, as is true of the Niobrara, Platte, Republican, and others. The result is not only that forest, scrub, and grassland are brought into the closest zonal juxtaposition, but also that there is a gradual shifting of the consocies, as the edaphic conditions of the river-bottom are modified by an increasingly arid climate. The developmental series previously indicated for the Otowanie Woods, namely, *Rhus, Fraxinus,* and *Quercus-Hicoria,* often with other consocies also, becomes a climatic series with exactly the same sequence from moist to dry conditions. Finally, the broad ecotones or transition areas between climax communities are clear indexes of the effect of climatic swings. They are mixed communities, and correspond closely to the mixture of two contiguous stages, *i. e.*, a mictium, in the course of succession.

Significance of alternation.—Alternation is the consequence of disturbed or incomplete zonation. Such areas produce *alternes*, which it now seems can always be related to more primary zones. This has already been shown in the case of the alternes of cañons, which are only the upward or downward extension of zones. Wherever the conditions which control zonation are disturbed, alternation is produced, just as is the case whenever the conditions for a particular zone occur abruptly or locally. An excellent example of the latter are the extra-regional pockets of *Celtis* or *Symphoricarpus*, described by Pool (1914) in the sand-hills of Nebraska. These are fragments of consocies, whose zonal relations are evident only where climatic conditions permit the development of forest. Similar detached thickets of *Cercocarpus* occur in the Wildcat Mountains of western Nebraska. Their proper relation can be understood only by a study of *Cercocarpus* as a consocies of the foot-hills of Colorado and Wyoming, where it is associated with *Quercus, Rhus,* and other shrubs. To *Quercus* and *Rhus trilobata* it bears a distinctly zonal relation, since it is the most xerophytic of the three, and consequently occupies knolls and ridges. The foot-hills, however, are so much dissected and bear so many outcrops of rock that the fundamental zonation is greatly interrupted, and in some cases thorough examination alone will disclose the fact that the numerous alternes are actually fragments of zones. The rolling character of the prairies has a similar effect. Ravines, gullies, and ridges of varying extent and rank are so numerous that zonation is often completely obscured and can be revealed only by tracing the distribution of characteristic species. This effect is enhanced by the many kinds of exposure and the ever-changing angle of slope and their effect upon both migration and ecesis.

Developmental relation of layers.—Fundamentally, layers are zones related to the decrease in light intensity from the primary layer toward the soil, though the increasing shade is really the reaction of the constituent species. Layering differs from zonation in being vertical instead of lateral and in giving a correspondingly complex structure to the community. Thus, while the developmental relation of layers is certain, it is not obvious. It is most evident in the layers of submerged, floating, and amphibious plants in water, since these are of course so many developmental stages and are associated only in mictia. The most typical development of layers is in forest, and this alone need be considered, since the less complete layering of grassland, herbland, and scrub is fundamentally similar. In the forest with a complete set of layers the latter indicate in a general way the sequence of life-form stages from the ground-layer of mosses and lichens through herb, grass, and shrub layers to the primary layer of trees. The species correspondence of layers and stages is usually slight or none, owing to the great difference in light intensity after the forest is established. However, a few species adapt themselves so readily that they persist for some time during the forest climax, and play a recognizable part in the constitution of layers. Such a result is indicated by the reciprocal fact that some species of the forest undergrowth are able to persist after the trees have been removed. In the spruce forests of the Rocky Mountains, *Opulaster* often persists to become the dominant species of the shrubby layer. In the final maturing of the spruce forest the number of layers is directly dependent upon the increasing density of the crown, and hence serves as a ready index of the degree of maturity, *i. e.*, of development.

The disappearance of the layers beneath the primary one follows the life-form sequence, but in the reverse order, the shrubby layer disappearing first, the bushes next, then the tall herbs, and last of all the ground herbs, the mosses and lichens remaining as the final remnant of the layered condition.

Relation of seasonal aspects.—In forest and thicket, aspects are due to the occurrence of societies at times when light conditions are most favorable. The prevernal aspect of deciduous woods is characterized by a ground-layer of species which develop before the woody plants unfold their leaves and before the other layers have appeared. In general, the herbaceous societies bloom and give character to the different layers in the order of height, so that the seasonal development recapitulates in some degree the succession of life-forms. The seasonal aspects of the prairie show a somewhat similar relation, though the cause is found in the water and heat as well as the light relation. The prevernal and vernal societies and clans are composed of low-growing herbs, such as *Anemone, Astragalus, Lomatium, Viola*, etc., which correspond to a ground-layer. The summer societies are tall-growing, and often allow the development of one or two layers beneath them. The serotinal aspect is likewise characterized by societies of tall plants, with at least partial secondary layers. Apart from the relation of the prairie aspects as layers, there is also a general developmental relation in that the conditions are nearest like those of meadow in the spring, and are most typical of the prairie in summer and autumn.

THE UNITS OF VEGETATION.

HISTORICAL SUMMARY.

The formation concept.—Although the detailed consideration of the structure of vegetation is reserved for another volume, it is desirable to consider here the chief concepts of the formation. No term has had a more varied experience or a larger variety of uses. Efforts to discard it have been futile, and attempts to definitize it of little avail. Like all plant structures, it is the outcome of development, and hence can not be absolutely delimited. The difficulties in its definition and use seem to have arisen from a failure to recognize its developmental character, as is shown later. As is true of all biological concepts, its first significance was necessarily superficial and incomplete. But the concept has broadened and deepened until, with the adoption of the developmental idea, it includes the whole group of relations between the basic unit of vegetation and its habitat. The history of the formation concept is the history of this process of refinement and definitizing.

Grisebach's concept of the formation.—As is generally known, Grisebach (1838:160) was the first to use the word "formation":

"The first method, the employment of which even a very superficial knowledge of a region makes possible, is based upon the physiognomy of vegetation, upon the grouping of individuals in the mass. I would term a group of plants which bears a definite physiognomic character, such as a meadow, a forest, etc., a phytogeographic formation. The latter may be characterized by a single social species, by a complex of dominant species belonging to one family, or, finally, it may show an aggregate of species, which, though of various taxonomic character, have a common peculiarity; thus, the alpine meadow consists almost entirely of perennial herbs. In a general account of the forma-

tions of a flora, it would be necessary to indicate the character plants and to determine the species to which they owe their physiognomic features, which are in no wise subjective. This is a task especially to be recommended to travellers, since it can be carried out easily and thoroughly. These formations repeat themselves everywhere in accordance with local conditions, but they find their absolute, their climatic limits with the natural flora, which they constitute. Just as far as forests of *Pinus silvestris* or heaths of *Calluna vulgaris* extend, just so far does one find himself in the region of the middle European flora. Even if a single species of one flora pass into another, a dominant species of a group does not appear at the same time in two floras. Every formation, whose character and components are indicated with distinctness, conforms to the limits of its natural flora."

From the above, it is obvious that Grisebach's conception of the formation was essentially if not wholly physiognomic. This was also true of the idea underlying Humboldt's use (1807:17) of the term *association*. While it is possible to find much harmony between the use of this term by Humboldt and by many modern writers, it seems obvious that Humboldt and Grisebach meant practically the same thing by their respective terms. Indeed, Moss (1910:21, 28) has already pointed out this fact in the case of both terms.

Drude's concept.—Drude (1890:28) has criticized Grisebach's concept and has insisted upon the necessity of considering the flora as of more importance than the physiognomy:

"Grisebach's definition of the formation must be taken in its entirety. It appears correct to regard the 'groups of plants, which bear a definite physiognomic character' as classes of formations. The occurrence of these and their extent permits one to distinguish the great vegetation zones of the earth, but they throw no light upon the question of floristic. Definiteness can be secured only by means of the latter, particularly if one considers that the special physiognomy is due simply to the dominant species, and without inventing a special physiognomic system. Therefore the essential task, in order to secure a general survey of the formations of a flora, is to determine their dominant species, and, one may add, to study their local conditions. Therefore I view the concept of formation in this later sense with reference to a particular flora.

"Hence, I regard as a vegetation formation, within the limits of a definite phytogeographic flora, each independent closed chief association of one or several life-forms, the permanent composition of which is effected by the definite conditions of the habitat, which keep it distinct from the adjacent formations."

Drude here clearly assigns a basic rôle to the habitat, but his actual delimitation of formations is based primarily upon floristic. He (1896:281, 286) further emphasized the necessity of taking the habitat into account in determining formations:

"The division of the vegetative covering appears to be determined by the arrangement of definite habitats, and coincides with the alternation of the principal plant communities, in which the physiognomic character of the land lies hidden. These concepts are designated as vegetation formations, which are the botanical units of the vegetative covering of the earth. . . . Every independent chief association which finds a natural end in itself and which consists of similar or related life-forms in a habitat with the same conditions

for existence (altitude, exposure, soil, water) is a vegetation formation. It is assumed that an essential change can not occur on the site of such a community without external changes: the community is 'closed.' "

Clements's concept.—Clements (1905:292) placed particular emphasis on the habitat as determining the formation concept and as affording a more accurate basis for recognizing and delimiting formations.

"In vegetation, the connection between formation and habitat is so close that any application of the term to a division greater or smaller than the habitat is both illogical and unfortunate. As effect and cause, it is inevitable that the unit of the vegetative covering, the formation, should correspond to the unit of the earth's surface, the habitat. This places the formation upon a basis which can be accurately determined. It is imperative, however, to have a clear understanding of what constitutes the difference between habitats. A society is in entire correspondence with the physical factors of its area, and the same is true of the vegetation of a province. Nevertheless, many societies usually occur in the same habitat, and a province contains many habitats. The final test of a habitat is an efficient difference in one or more of the direct factors, water-content, humidity, and light, by virtue of which the plant covering differs in structure and in species from the areas contiguous to it. This test of a formation is superfluous in many cases where the physiognomy of the contiguous areas is conclusive evidence of their difference. It is also evident that remote regions which are floristically distinct, such as the prairies and the steppes, may possess areas physically almost identical, and yet be covered by different formations."

This concept of the formation recognized both the physiognomic and floristic sides, but assigned the chief value to the habitat because of its fundamentally causative character. The habitat was regarded as something to be measured and studied exactly, with the object of determining the causes of the development and structure of communities, and hence arriving at the real limits of the formation and its divisions.

Moss's concept.—Moss (1907:12) was the first to take development into account in determining formations:

"A plant association in which the ground is carpeted in this sparse manner, with patches of bare soil here and there, is spoken of as an open association. An open association represents an early stage in the succession of associations which finally lead to a closed association, when the ground is fully occupied by one or a very few dominant plants, and a period of stability of vegetation has been reached. The series of plant associations which begins its history as an open or unstable association, passes through intermediate associations, and eventually becomes a closed or stable association, is, in this paper, termed a plant formation."

Moss (1910:35, 36) states in a later paper that he:

"Followed many previous authors in delimiting formations primarily by habitat, and then subdividing the formations into associations. This writer laid stress upon the succession of plant associations, especially on the succession of associations within the same formation. It is necessary to distinguish the series of associations within a whole succession, that is, the succession from one formation to another, and the succession of associations within one and the same formation; and Moss enunciated a statement of the formation from the latter point of view."

As indicated above, Moss's intention was to base formations primarily upon habitat. Since he regarded the latter chiefly in the light of soil relations, it was inevitable that he should group together in the same formation the seral associations, such as forest, scrub, and grassland, which are due to efficient differences of light and water-content. As a consequence, Moss's concept of the formation was only incidentally developmental, and his actual formation is a different thing from the climax formation. While the latter is the outcome of development, it consists of two or more related climax associations, and not of a climax association plus two or three antecedent developmental associations. The views of Moss in regard to the formation were adopted by Moss, Rankin, and Tansley (1910) and by Tansley (1911).

Schröter's concept.—Schröter (1902:68) has traced the outlines of a topographic-physiognomic system of formation groups. The unit of this system is the local association, which characterizes a definite locality of uniform habitat. The diagnosis of the formation unit comprises (1) locality, (2) habitat, and (3) plant-cover, (*a*) physiognomy, (*b*) life-forms, (*c*) list of species. A formation comprises all the association types of the entire earth, which agree in their physiognomy and ecological character, while the floristic is immaterial. The series of units is as follows:

I. Type	Vegetation type	Grassland.
II. Formation	Formation group	Meadow.
	Formation	Dry meadow.
	Subformation	Alpine dry meadow.
III. Bestand	Association type	*Nardetum.*
	Subtype	*Nardetum* with *Trifolium.*
	Facies	*Nardetum* (*Nardus* dominant).
	Local association.	*Nardetum* at Gotthard.

In contrast to Schröter's topographic-physiognomic concept, Brockmann-Jerosch (1907:237) considers the first task in the study of plant communities to be their limitation and description upon a physiognomic-floristic basis. The author expressly refrains from defining his concept of formation and association, but the essence of it is readily gained from the argument. In spite of the difference of emphasis upon habitat and floristic, the viewpoints of Schröter and Brockmann are very similar. They both accept the "pigeonhole" concept of the formation proposed by Warming and justly criticized by Moss.

Gradmann's concept.—Gradmann (1909:97) has also emphasized the importance of floristic at the expense of other criteria:

"Since the physiognomic and ecological viewpoints have been shown inadequate for a botanical distinction, there remains the sole possibility of grounding formations upon their floristic composition. In fact, the floristic method is the only one which can be completely carried out in a monographic treatment of formations. Many a well-marked and natural formation can be distinguished in no other way than by its floristic composition. On the other hand, every formation determined by physiognomic characters can be circumscribed just as well floristically. At the most one thereby obtains somewhat smaller units, which is by no means unfortunate, since it indicates nothing else than greater accuracy. As a consequence, floristic studies are always a substitute for pure physiognomic or ecological viewpoints, but the converse is

not true. Moreover, the floristic method has the advantage of being purely analytical and hence highly objective. It is independent of physiological theories and does not presuppose a knowledge of causal relations, but leads up to it. It permits one to reckon with habitat and adaptations, as well as with unknown factors; it proposes problems, and it stimulates to new investigations and advances. Through refining this method of determining the controlling factors by means of floristic agreements and contrasts, one can certainly obtain much insight into the factors of plant life, which have heretofore been overlooked. Thus, while the floristic analysis stands out as the most exact, most objective and most fruitful, and indeed as the sole universally applicable expression of the formational facts, yet it in no wise excludes the consideration of other viewpoints, but on the contrary encourages their use. Nothing stands in the way of adding to the floristic characterization a thorough analysis and description of the environic, physiognomic, ecologic, phytogeographic, and developmental relations. The chief emphasis must fall upon these fundamental investigations and for these the floristic has only to furnish a basis free from objections. But such viewpoints can not serve for the limitation of formations; moreover, there is nothing to be gained from dubious and arbitrary compromise. I hold therefore that we must universally recognize the floristic composition not merely as an important, but much rather as the basic and decisive criterion for the recognition of plant formations."

Warming's concept.—Warming (1895) assigned to the habitat the chief value in determining plant communities. As he rejected the term "formation," however, it is impossible to obtain his concept of the formation at this time. In the second edition of his pioneer work (1909:140), he expresses the concept as follows:

"A formation may then be defined as a community of species, all belonging to definite growth forms, which have become associated together by definite external (edaphic or climatic) characters of the habitat to which they are adapted. Consequently, as long as the external conditions remain the same, or nearly so, a formation appears with a certain determined uniformity and physiognomy, even in different parts of the world, and even when the constituent species are very different and possibly belong to different genera and families. Therefore—

"A formation is an expression of certain defined conditions of life, and is not concerned with floristic differences.

"The majority of growth forms can by themselves compose formations or can occur as dominant members in a formation. Hence, in subdividing the groups of hydrophilous, xerophilous, and mesophilous plants, it will be natural to employ the chief types of growth forms as the prime basis of classification, or, in other words, to depend upon the distinctions between trees, shrubs, dwarf-shrubs, undershrubs, herbs, mosses and the like."

Moss (1910:39) has criticized Warming's concept of the formation, which treats the latter as a subjective group comprising all associations of like physiognomy. He considers that:

"Warming has given the concept an unfortunate bias, and that his view is sufficiently at variance with historical and present-day usage to demand some examination of his treatment of this unit of vegetation. Confusion is apparent even in Warming's summary statement of the formation. Instead of a single *fundamentum divisionis*, Warming puts forward two tests of the formation, namely, definite plant forms ('growth-forms') and definite characters of the

habitat. It is not clear, either from his definition or from his general treatment of formations, what Warming precisely means by the term 'definite growth-forms.' In any case, the definition is defective, as plant form is not necessarily related to habitat: and therefore the two tests put forward in the one definition will frequently yield contradictory results. Warming (p. 232) insisted that a salt marsh characterized by suffruticose Salicornias 'must be set apart from' salt marshes characterized by herbaceous Salicornias 'as a separate formation' merely because the plant form in the two cases is different. Such paradoxes occur throughout the whole of Warming's book; and indeed this Janus-like 'formation' is inevitable if plant form is to be allowed to enter into competition with habitat in the determination of formation. Warming's view might find some justification if definite plant forms were invariably related to definite habitats; but it is quite certain that this is not the case. For example, on salt marshes in the south of England, it is no unusual thing to find associations characterized (*a*) by herbaceous species of *Salicornia*, (*b*) by suffruticose species, and (*c*) by a mixture of these. To place these associations in separate 'formations,' however, simply because of the different nature of the plant forms, is to reduce the study of formations to an absurdity."

The foregoing criticism is as valid from the developmental viewpoint as from that of the habitat. It brings out in clear relief the fallacy of using a single basis for the recognition of formations, as is the usual method in most systems, notwithstanding statements to the contrary in defining the concept. There is of course no real contradiction between habitat and physiognomy, in spite of the fact that two or more life-forms may appear in the same habitat, and that the same life-form may recur in widely different habitats. The error lies in assuming that all species must make the same structural responses to a habitat, and that the general character of the life-form necessarily indicates its actual response. Nowhere in the field of ecology is there a more striking confirmation of the fact that development is the sole clue to follow through the maze of apparent and real, of superficial and basic relations between habitat, floristic, and physiognomy.

Moss (1910:39) commends Warming for adopting, in connection with the division of the formation into associations, "a view which has forced itself on the minds of nearly all close students of vegetation." This is the view of Cowles (1899:111), in which he regarded the relation between the formation and association as similar to that of the genus to the species. The wording of Cowles's statement is as follows: "One might refer to particular sedge swamp societies near Chicago, or to the sedge swamp formation as a whole; by this application, formation becomes a term of generic value, plant society of specific value." It is an open question whether the relation of particular local associations to an actual floristic entity is not really intended. In any event, it seems clear that there was no expressed intention of building up an artificial concept like the genus by placing in it all the swamp associations of the entire globe. Yet this is a legitimate if not necessary assumption from this comparison, and it is illogical to commend the acceptance of the principle and to object to the application of it. In the meaning of formation as used by those who regard it as a definite entity, the sole relation of the genus to the species that is shown by formation and association is that of a division and its subdivision.

Negri's concept.—Negri (1914:33) has advanced a novel concept of formation and association, in accordance with which they become merely different viewpoints of the same thing:

"We term formation this vegetation considered in the complex of its biological relations, but not in its floristic composition; and understood in the totality of its individuals and in all the secondary variations of composition, of arrangement and of frequence, which it undergoes during the persistence of a physiographic unit of essentially unchanged edaphic conditions. (33) The formation is the physiognomic and ecologic expression of the association, as the biologic form is the physiognomic and ecologic expression of the species. (41) To the formation—biologic term—corresponds exactly the association—floristic term." (44)

The adoption of this concept would result in the loss of the one point upon which practically all ecologists are in agreement, namely, the subordinate relation of the association to the formation. There can be no question of the need of physiognomic, ecologic, and floristic viewpoints of the formation, but their real values and significance appear only as they are considered in relation to development. The author's failure to understand the fundamental nature of the formation as an organism with its own development is further indicated by his comment upon climax formations. (42) While it is quite possible to give the formation a different name for each of the four criteria, viz., development, physiognomy, habitat, and floristic, it is clearly inadvisable to do so. This is not merely because of the deluge of names that would result, but especially because of intimate and often inextricable relations of these four elements.

Correlation of divergent views.—The extreme range of opinion as to the concept of the formation is afforded by the views of Gradmann and of Warming. The one would "ground formations solely upon floristic," the other expressly states that the "formation is not concerned with floristic." Both clearly demonstrate that a partial view is unfortunate, and serve to convince the open-minded student that only the complete point of view, which includes all of the relations of habitat and formation, is scientifically tenable. Every investigator has been concerned primarily with one relation and has minimized or neglected all the others. As a consequence, every standpoint has had its vigorous advocates, with the result that their arguments have proven each other partly right and partly wrong. It is clear why physiognomy as the most obvious basis should have first dominated the concept, and why it should have been displaced more and more by floristic. In both cases the habitat could not well be completely ignored, but its real value could be appreciated only after it began to be studied by means of instruments. Development is the most recent phase of formational study, and has in consequence played little part in determining the concept. The recognition of its fundamental rôle in no wise minimizes the importance of the other viewpoints, since it is an epitome of them all. It is also true that habitat, floristic, and physiognomy are complementary and not antagonistic. A complete picture of the formation is impossible without all of them, and the question of relative importance, if of any consequence at all, is a matter for much more detailed and thorough investigation than we have had up to the present.

Hence there is here no intention of setting up another antagonistic concept of the formation, *i. e.*, one based upon development. The **actual recognition of formations** by means of physiognomy, of floristic, and of habitat has been tried repeatedly by the use of detailed and exact methods of quadrat and instruments. This has afforded conclusive proof that no one of the three viewpoints is adequate alone or primarily. This conclusion is reinforced by the conflicting opinions of the advocates of the different concepts, but especially by the intensive study of the interrelations of community and habitat. Every community not only owes its grouping or composition to the habitat, but the species, and especially the dominant ones, take their characteristic impress from it. While their reproduction-form or taxonomic form shows this least for obvious reasons, the vegetation-form, growth-form, or life-form usually affords a striking illustration of this fact, and the habitat-form is an exact and universal record of it. On the other hand, the community modifies the habitat materially or essentially by its reactions upon it, and the habitat thus changed has a new action in selecting and modifying the species which enter it. This maze of action and reaction continues from the beginning to the end of the life-history of the formation, and it is as one-sided and unfortunate to emphasize one precess as it is the other. The habitat is the basic cause, and the community, with its species or floristic, and its phyads and ecads, or physiognomy, the effect. But the effect in its turn modifies the cause, which then produces new effects, and so on until the climax formation is reached. A study of the whole process is indispensable to a complete understanding of formations. One must perforce conclude that the results obtained from the over-emphasis of physiognomy, floristic, or habitat are as incomplete as the concept itself. The simultaneous study of all the processes and facts can not yield too much truth, and it is a distinct handicap to assume that a single viewpoint can afford all or most of the truth.

Significance of development.—It is for these reasons that development is taken as the basis for the analysis of vegetation. It is not a single process, but a composite of all the relations of community and habitat. It not only includes physiognomy, floristic and habitat, but it also and necessarily includes them in just the degree to which they play a part, whatever that may be. Development furnishes, not a new point of view more or less incomplete and antagonistic to those already existing, but one which includes all the others and harmonizes and definitizes them. Its importance is just as great and its use just as fundamental as in taxonomy. The artificial system of Linnæus was not unnatural because it failed to use natural characters, but because it used only part of them, and these not in their most fundamental relations. So, likewise, all the concepts of the formation and the methods of recognition so far employed are natural in so far as they use a natural process or response, and artificial in so far as they fail to correlate this with all the other equally natural and important processes. Taxonomic systems have become natural and hence fundamental in just the proportion that it has been possible to ground them upon development. Development is likewise the only basis for a natural system of formations. It is as indispensable to their recognition as to their classification.

Earlier suggestions of the developmental view.—The fact that development has more than once been used in classifying communities indicates that

the idea has not been wholly ignored in the formational concept. All of the writers upon retrogression and regeneration of communities have had an inkling of this fact, but have nowhere expressed it in the formational concept. Drude suggests the idea more or less incidentally in his definitions (1890: 29; 1896:286) when he speaks of a formation reaching an end in itself. Pound and Clements (1898:216; 1900:315) distinguished formations as either primitive or recent with respect to origin, and stated that formations originate at the present day by one of two principal methods, by nascence or by modification. Schimper's (1898) much-discussed division of formations into climatic and edaphic was really based upon development, but he failed to recognize the fundamental and universal nature of edaphic formations as processes of development. In his physiographic ecology, Cowles (1901) dealt primarily with development, though this fact was obscured by the emphasis laid upon physiography. However, he used the term "society" in place of "formation," and his developmental ideas were not embodied in the formational concept. Clements (1902; 1904:6; 1905:199; 1907:219) advanced the concept that the formation was essentially developmental in character, and stated that it may be regarded as a complex organism which shows both functions and structure, and passes through a cycle of development similar to that of the plant. Transeau (1905:886) also adopted a similar view in the statement that "each formation is made up of many societies, bearing a definite successional relation to one another." He made no concrete applications of his view, and hence it remains ambiguous. Moss (1907:12; 1910:36) proposed a view similar to the two preceding, in which, however, the limitation of the formation was grounded primarily upon the habitat. Tansley (1911:9) has adopted Moss's concept, and defines the formation as follows:

"In the normal primary development of a formation, the associations involved show intimate relations and transitions one to another, and the whole set of associations has a definite flora dependent on the type of soil. It is for these reasons that we consider the entire set of plant communities on a given type of soil, in the same geographical region, and under given climatic conditions, as belonging to one formation, in spite of the diversity of the plant forms in the different associations. The plant formation thus appears as the whole of the natural and semi-natural plant-covering occupying a certain type of soil, characterized by definite plant communities and a definite flora."

As has elsewhere been shown, the developmental value of this concept has been greatly reduced by linking the habitat to a type of soil.

THE FORMATION.

Developmental concept of the formation.—In spite of the growing tendency just indicated, no attempt has hitherto been made to put the formation either chiefly or wholly upon a developmental basis. While this view has been stated and restated in the preceding pages, it seems desirable to repeat it here at some length. The unit of vegetation, the climax formation, is an organic entity. As a complex organism, the formation arises, grows, matures, and dies. Its response to the habitat is shown in processes or functions and in structures which are the record as well as the result of these functions. Furthermore, each climax formation is able to reproduce itself, repeating

with essential fidelity the stages of its development. The life-history of a formation is a complex but definite process, comparable in its chief features with the life-history of an individual plant. The climax formation is the adult organism, the fully developed community, of which all initial and medial stages are but stages of development. Succession is the process of the reproduction of a formation, and this reproductive process can no more fail to terminate in the adult form in vegetation than it can in the case of the individual plant.

The underlying causes of complete development of the formation are to be sought in the habitat, just as they are in the case of the individual. The significant difference lies in the fact that the reactions of the individuals as a community produce a cumulative amelioration of the habitat, a progressive improvement of the extreme, intrinsic to the continuance of development itself. The climax formation is thus a product of reaction operating within the limits of the climatic factors of the region concerned. A formation, in short, is the final stage of vegetational development in a climatic unit. It is the climax community of a succession which terminates in the highest life-form possible in the climate concerned.

Analysis of the formation.—Just as development determines the unit of vegetation to be the climax formation, so it also furnishes the basis for recognizing the divisions into which the formation falls. It is evident that the final stage of a sere differs from all the preceding ones in a number of respects, but chiefly in being fixed throughout a climatic era. It is in essential harmony with its habitat, and no change is possible without a disturbance from the outside. Its own reaction is neither antagonistic to itself nor more favorable to other species. In the case of all the other successional stages, their respective communities persist for a time only because their lack of harmony with the climatic conditions is counterbalanced by a more or less extreme set of edaphic conditions. Sooner or later this compensating relation is destroyed by the progress of the reaction, and the one stage is replaced by another. As a consequence, the formation falls naturally into climax units or associations, and developmental or seral units, associes. The former have their limits in space, and are permanent for each climatic era; the latter are limited in time, and they arise and pass in the course of successional development. Seral units represent the visible or determinable stages of development, and hence include all the successive communities of a sere. Each associes is based in consequence upon population, life-form, and habitat, though it is most readily distinguished by means of its dominant species. It is not certain that the major changes in dominance and life-form coincide with the major changes of the habitat, but quantitative studies point more and more to this conclusion.

Formation units.—Moss (1910:20, 27) has traced in detail the development of the concepts of formation and association, as well as their varying use, while Flahault and Schröter (1910) have made an illuminating summary of them in connection with phytogeographic nomenclature. The first endeavor to analyze these units more minutely was made by Clements (1905: 296, 299), who proposed *society, community,* and *family* as respective subdivisions of the association. A similar division of the formation into types, facies, aspects, and patches had been made by Pound and Clements (1898: 214; 1900: 319) and Clements (1902:19), but the essential nature of the type

as a subdivision of the formation was obscured by a double use of the latter term. The term *society* was adopted by Moss (1910) and Tansley (1911), and has been used more or less generally by British ecologists. The latter have also tended to employ *community* as an inclusive term for any and all units from the formation to the family. Convenience and accuracy demand such a term, and it is here proposed to restrict community to this sense. For its concrete use to designate the division next below the society, the term *clan* is proposed.

The term *consocies* was first proposed (Clements, 1905:296) as a substitute for association, owing to the use of the latter in both an abstract and a concrete sense. The general use of association in the concrete sense has fixed it definitely in ecological terminology. At the same time, its actual application to particular communities has shown the widest divergence of viewpoint. As a consequence of more exact knowledge of vegetation, it became evident that a new division was needed between association and society to designate the characteristic dominance of facies (Pound and Clements, 1900:319). The term *consocies* has been used for this division, since this is precisely the unit for which it was first proposed. Thus, while the relation of formation and association remains the same, consocies would become the term to be applied to by far the larger number of associations as hitherto recognized. This concept in particular has been repeatedly tested during the past two years throughout the western half of North America, and has shown itself to be one of the most valid and easily applied of all the units. The term has been used in this sense or essentially so by Shantz (1906:36), Jennings (1908:292; 1909:308), Gleason (1910:38), Gates (1912:263), Matthews (1914:139), and Vestal (1914:356; 1914:383) (plate 35 opposite).

However, the requirements of a developmental analysis of vegetation make it desirable, if not necessary, to distinguish between climax and developmental consocies. Accordingly, it is proposed to retain consocies for the seral unit, and to employ *consociation* for the climax unit. Thus, from the standpoint of structure, the following plant communities are recognized, namely, formation, association, consociation, society, clan, and family. Their essential relationship is indicated by the sequence. Since at least the formation, consociation, and family permit of objective limitation, the use of the remaining terms may be definitized much more than has been the case hitherto.

Formation.—The formation is the unit of vegetation. It is the climax community of a natural area in which the essential climatic relations are similar or identical. It is delimited chiefly by development, but this can be traced and analyzed only by means of physiognomy, floristic, and habitat. In a natural formation, development, physiognomy, and floristic are readily seen to be in accord, but this often appears not to be true of habitat. There are several reasons for this. In the first place, complete and exact knowledge of any habitat is still to be obtained. As a consequence, the actual correlation of factors and the critical responses of the plant are as yet untouched. Finally, we think of climate in human terms, and forget that the only trustworthy evidence as to climatic climaxes must be obtained from the responses of the plant and the community. Even the exact evidence obtained by recording instruments may be most misleading, unless it is translated into terms of plant life. Thus, while there is every certainty theoretically that the respon-

sive unit, the formation, is in harmony with the causal unit, the habitat, our present knowledge is inadequate to prove this. As a consequence, the habitat can only be used in a general way for recognizing formations, until we have a much clearer understanding of the climatic and edaphic factors and the essential balance between them.

The developmental limitation of formations demands long investigation. Hence it is necessary to appeal first to physiognomy and floristic for tentative units, except in regions where successional studies are already well advanced. Such tentative units must be tested and confirmed by development before they can be accepted. Such a test will necessarily involve the use of habitat criteria to an increasing degree. Thus, over the whole of the Great Plains region, life-forms and population indicate a vast grassland formation. The existence of such a climax is confirmed by numerous developmental studies which have already been made upon it. In the matter of temperature the region is far from uniform, but in the critical water relations investigation shows it to be essentially a unit. Over this wide stretch from Texas and northern Mexico far into Alberta, the dominant genera are the same, and this is true of many of the species. This is also true of the genera and some of the species of the scrub or chaparral formation which extends from Minnesota westward to British Columbia, southward to California and Mexico and eastward to Texas, Colorado, and Nebraska.

According to the developmental idea, the formation is necessarily an organic entity, covering a definite area marked by a climatic climax. It consists of associations, but these are actual parts of the area with distinct spatial relations. The climax formation is not an abstraction, bearing the same relation to its component associations that a genus does to its species. It is not a pigeon-hole in which are filed physiognomic associations gathered from all quarters of the earth. Hence it differs radically from the formation of Warming and other writers who have adopted his concept. According to the latter (1909:140; *cf.* Moss, 1910:43), "a formation appears with a certain determined uniformity and physiognomy, even in different parts of the world, and even when the constituent species are very different and possibly belong to different genera and families. Therefore a formation is an expression of certain defined conditions of life, and is not concerned with floristic differences." The formation as developmentally limited would include the closely related chief associations of Drude (1896:286) and Moss (1910:38). The formations of many writers are associations as here understood, and those of Hult and his followers are mostly consocies and societies. The current conceptions of formation and association in the larger sense were regarded as fairly final by the writer, until 15 months of continuous field-work in 1913 and 1914 made this position appear to be no longer tenable. This change of view was not only a direct consequence of the application of developmental principles to a wide range of communities, but it was also rendered unavoidable by the opportunity of comparing all the formations and associations in the region from the prairies to the Pacific Coast, and between Mexico and middle Canada during the summer of 1914.

Names of formations.—The need of being able to designate formations more accurately than by the use of vernacular names led to the proposal by Clements (1902:5) that they be designated by Greek names of habitats or

communities, to which the suffix, *-ειον, place,* was added. This suggestion has been adopted by Ganong (1902:53; 1903:303), Diels (1908:70; 1910:18), and Moss (1910:142; 1913:167). More recently, Brockmann and Rübel (1912), and Rübel (1915) have proposed a physiognomic system based upon Latin. The physiognomic basis seems much less satisfactory, and the use of Latin compounds certainly leaves much to be desired in the matter of uniformity, brevity, and euphony. While Clements and Diels use the transliterated form of the suffix, as in *hylium, helium,* etc., Moss objects to this because of the fear that it would lead to confusion with neuter generic and specific names. Such confusion would be impossible if the formational terms are not capitalized, as was originally intended. Since uniformity is more desirable than any other feature of terminology, the modification of the term by Moss is accepted here, as it has become more or less current in British publications. Since climax formations are clearly dependent upon the flora, it seems impossible to ignore this fact in the name. Moss objects to the use of the names of dominant genera, as in "Eriophorum-Scirpus oxodion," because it is not really definitive, as no indication is given of the species of *Eriophorum* or *Scirpus.* Further objection is raised because the oxodion comprises not merely the two associations designated, but probably at least two dozen. These objections disappear in the developmental treatment of formations, since there are rarely more than a few associations in a formation. If *Bulbilis-Bouteloua-poion* is thought too long for the name of the short-grass climax of the Great Plains, it can be called simply *Bouteloua-poion,* just as a similar climax elsewhere might be the *Stipa-poion.* The greater definiteness both as to floristic and region seems to render such formational names preferable to Moss's *α-oxodion, β-oxodion,* etc.

CLIMAX UNITS.

Association.—The association has had as varied a history as the formation. Not only has the one been used for the other, but even when they have been employed in the proper relation the units to which they have been applied have varied greatly. As has been already indicated, the association as usually understood becomes what is here termed the consociation, in so far as it is a climax community. This is the association with a single dominant. While many associations of two or more dominants have been recognized, these are practically all what Moss (1910:38) terms *subordinate associations,* that is, successional communities or associes (plate 15, A, B).

The association as here conceived bears the accepted relation to the formation. The term is restricted, however, to those climax communities which are associated regionally to constitute the formation. The associations agree with their formation in physiognomy and development, but differ in floristic and to a certain though unknown degree in habitat. Hence they are recognized chiefly by floristic differences. Associations are marked primarily by differences of species, less often by differences of genera. At the same time, their organic relation to each other in the climax unit or formation rests upon floristic identity to the extent of one or more dominants, as well as upon the fundamental development and the life-forms. For example, the *Bouteloua-poion* contains two associations, the *Bulbilis-Bouteloua-association,*

and the *Aristida-Bouteloua-association.* While the species of *Bouteloua* and *Aristida* are mostly different in the two, one or more species of both genera are more or less common throughout. In the scrub or chaparral formation, *Quercus, Ceanothus, Cercocarpus,* and *Rhus* are common genera, with one or more common species. Associations show a similar relationship with reference to the principal and secondary species. The great majority of these are the same as to genera, and the number of identical species is usually considerable.

From the organic connection between formation and association, it seems desirable to use similar terms to designate them. For the sake of distinction, however, it is necessary to employ the termination in different form. Accordingly, it is proposed to use the roots found in *hylion, helion, poion,* etc., but to substitute the ending *-ium* for *-ion*: Thus, the short-grass formation, *Bouteloua-poion,* of the Great Plains would fall into the *Bulbilis-Bouteloua-poium* and the *Aristida-Bouteloua-poium.* This method has the advantage of definitely correlating formation and association upon the basis of life-form and habitat, and of reducing the number of terms needed. The names thus constituted are so few and so distinctive that there seems not the slightest danger of confusion with neuter generic names (cf. p. 182).

Consociation.—The consociation is the unit of the association. It is characterized by a single dominant. The association is actually a grouping, the consociation is pure dominance. Hence it is the most readily recognized of all communities, and it has figured both as formation and association. In the usual treatment most consociations appear as associations. This fundamental relation between formation, association and consociation was recognized by Pound and Clements (1898:223, 1900:324) in the division of the river-bluff formation into the red oak-hickory type, and the bur oak-elm-walnut type, each characterized by a number of dominant species or facies. While the communities are now seen to have been too restricted, the sequence of formation, type, and facies is essentially that of formation, association and consociation. A similar relation between the facies and consocies was recognized by Clements (1907:226). As a consequence, it is but a short step to clarify this relation into the exact one here established between association and consociation. The association thus becomes a group of two or more consociations, and the word "facies" disappears in this sense at least.

The uniform dominance of a consociation makes its recognition a simple matter. Since the consociations of an association approach each other in equivalence, *i. e.,* in response to the habitat, they are frequently mixed in various degrees. Such mixtures are more or less complete expressions of the association, however, and are so numerous and various that no definite term is required. The *Bulbilis-Bouteloua-poium* consists of two divisions, the *Bouteloua consociation* and the *Bulbilis consociation;* the *Aristida-Bouteloua-poium* of several consociations, *Bouteloua rothrockii, B. eriopoda, Aristida, arizonica,* etc. When two or more consociations are mixed, the term *mictium* (Clements, 1905:304) may be employed when needed, as for example, a *Bubilis-Bouteloua-mictium* would be an area of mixed grama and buffalo-grass, which, with the *Bouteloua* and *Bulbilis* consociations, would make up the association. Such a mictium is, however, only the association in miniature.

A. Montane forest association, *Pinus-Abies-hylium* (*P. ponderosa*, *P. lambertiana*, *A. concolor*), Yosemite, California.
B. Yellow-pine consociation, *Pinetum ponderosae*, Prospect, Oregon.

A consociation is denoted by the term *-etum,* a suffix long ago proposed by Schouw (1823:165) for a community characterized by a single dominant. This termination has come into general use, usually for a single dominant, though frequently for a group of related or associated dominants. It is here restricted to the climax community formed of a single dominant, *i. e.*, the consociation, for example, *Boutelouetum, Bulbiletum, Aristidetum, Quercetum, Rhoetum,* etc.

Society.—The society is a community characterized by a subdominant or sometimes by two or more subdominants. By a subdominant is understood a species which is dominant over portions of an area already marked by the dominance of consociation or association. The society is a localized or recurrent dominance within a dominance. In the case of grassland, the striking subdominance of many societies often completely hides the real dominance of the consociation. In forest, societies are found only beneath the primary layer of trees, and their subdominance is obvious. The society comes next below the consociation in rank, but it is not necessarily a division of it, for the same society may extend through or recur in two or more consociations, *i. e.*, throughout the entire association. This seems readily understandable when we recognize that the life-forms of the society subdominants are regularly different from those of the dominants of grassland and forest. The societies of grassland are composed of herbs or of undershrubs rather than grasses, those of woodland, of herbs, bushes, and shrubs. They may occur more or less uniformly over wide stretches, or they may be repeated wherever conditions warrant (plate 16 A).

The concept of the society was proposed by Clements (1905:296) and was defined as follows:

"The seasonal changes of a formation, which are called aspects, are indicated by changes in composition or structure, which ordinarily correspond to the three seasons, spring, summer, and autumn. The latter affect the facies [consociations] relatively little, especially those of woody vegetation, but they influence the principal species profoundly, causing a grouping typical of each aspect. For these areas controlled by principal species, but changing from aspect to aspect, the term *society* is proposed. They are prominent features of the majority of herbaceous formations, where they are often more striking than the facies. In forests they occur in the shrubby and herbaceous layers, and are consequently much less conspicuous than the facies."

Later (1907:226), the concept was somewhat broadened:

"An area characterized by a principal [subdominant] species is a society. A society, moreover, is often characterized by two or more principal species. Societies have no essential connection with consocies. A consocies may include several or many societies, or it may not show a single one. Finally, a society may lie in two consocies, or it may occur in any of them."

Tansley (1911:12) and his co-workers have adopted the concept of the society, and have stated it as follows:

"Locally within an association there occur more or less definite aggregations of characteristic species or of small groups of species, and these, which appear as features within the association, may be recognized as smaller vegetation units, or *plant-societies.* Sometimes their occurrence may be due to local variations of the habitat, at other times to accident and the gregarious

habit originating from a general scattering of seed in one place, or from the social growth of a rhizomic plant. It is a question whether it would not be better to separate these two causes of the production of societies within an association, and to restrict the term society to aggregations due to the latter alone. In this way we should obtain a more logically coherent conception. But the more detailed analysis of vegetation has hardly progressed far enough at present to justify a finer classification of plant communities. While a plant formation is always made up of associations, an association is not always or even necessarily made up of societies, which are essentially local discontinuous phenomena. Finally, plant-societies are minor features of vegetation, and their presence in certain spots is generally determined by some biological peculiarity, not by the habitat as such."

Moss (1910:48) states that "it is becoming usual in this country to speak of the subdivisions of the association as plant societies (*cf.* Clements, 1905:296)," and (1913:19) that "a plant society is of lower rank than an association, and is marked by still less fundamental differences of the habitat." The facies and "*nebenbestände*" of many authors are societies, as are also many of the patches of Pound and Clements (1898:214; 1900:313) and Clements (1902:19). The concept of the society has further been adopted and applied by Shantz (1906:29; 1911:20), Young (1907:329), Jennings (1908:292; 1909:308), Ramaley (1910:223), Adamson (1912:352), and Vestal (1914[2]:383).

Bases.—While the concept of society arose from the dominance of principal species, and thus has always had more or less relation to seasonal aspects, there is no necessary connection between the two. In the prairie association the seasonal appearance of societies is a marked phenomenon. In other communities the four aspects, prevernal, vernal, æstival, and autumnal, may be reduced to two or even one, and a society may then persist through much or all of the growing season. Even when the aspects are well-marked, a particular society may persist through two or more. As a consequence, the question of time relations is not a necessary part of the concept, though it may prove desirable to distinguish societies with marked seasonal character.

The real warrant for the recognition of societies lies in the structure, and hence in the development of the formation also. Areas of characteristic dominance occur within the major dominance of consociation and association. Such communities can not be ignored, for they are just as truly a part of the plexus of habitat and vegetation as the consociation itself. They are an essential result of the interaction of physical and biological processes, and the explanation of their occurrence is necessarily to be sought in the habitat. As Tansley has suggested (1911:12), it may prove desirable to distinguish societies controlled by obvious differences of habitat from those in which such control is lacking or obscure. This seeems a task for the future, however, since it depends primarily upon the instrumental study of units, of which we have the barest beginning. Moreover, it appears evident that the vast majority of societies, if not all of them, are expressions of basic habitat relations. This must certainly be true of the societies of climax associations and consociations, and it must also be the general rule in the case of the developmental societies of a sere. The only obvious exceptions are furnished by ruderal or subruderal species which invade quickly and remain dominant for only a few years. In

the Great Plains the societies of *Eriogonum, Psoralea, Helianthus,* etc., which occur and recur over thousands of square miles, have had abundant time and opportunity to migrate over the whole region; *Psoralea tenuiflora* is found, in fact, from Illinois and Minnesota to Texas, Sonora, Arizona, and Montana. Hence the presence of the society over large stretches and its absence in other places must be a matter of habitat control. In this, naturally, competition must often play a dominant part, and there can be little question that exact analysis will some day enable us to distinguish some societies upon this basis (Woodhead, 1906:396; Sherff, 1912:415). At present, such a distinction is impossible or at least without real meaning. Hence, while societies are readily seen to range from complete dominance, often greater than that of the consociation, to mere characteristic, it is highly probable that these merely represent different degrees of habitat response. This is often not obvious, for the decisive effect of the factors which control a society may be felt only at the time of germination for example, and might easily escape one who failed to use the exact methods of quadrat study throughout the entire growing-season. Perhaps no better evidence of the relation of societies to habitat can be furnished at present than their striking variation in abundance from one area to another, when such areas show no visible habitat differences. As a consequence, while it is possible to regard some societies as dominant, and others as only characteristic, it is felt that such a distinction is merely one of degree. It is necessarily superficial in the present state of our knowledge, and has the further disadvantage of being too easily subjective. An experimental study of dominance might well furnish a real basis for distinctions here, but further analysis must await such study.

Kinds of societies.—There may well be differences of opinion as to the desirability or necessity of distinguishing various types of societies. Those who are more interested in other phases of vegetation than in its development and structure will naturally not need to use finer distinctions. On the contrary, those who wish to trace in detail the response of the community to its habitat will find it helpful to recognize several kinds of societies. Even here, however, it is undesirable to outrun our present needs and to base distinctions upon differences which are subordinate or local. Thus, while it is convenient and natural to recognize layer societies, it would result in a surplus of concepts and terms to distinguish societies upon the basis of the six or eight layers present in well-lighted forests. Accordingly it seems desirable to regard all societies as due to habitat control, more or less modified by competition, and to establish subdivisions only upon the following bases: (1) aspects, (2) layers, (3) cryptogams. In addition, there are the relict and nascent societies of various seral stages, which will be considered under developmental societies. Finally, there are the related questions of changes of rank or dominance, which are dealt with below.

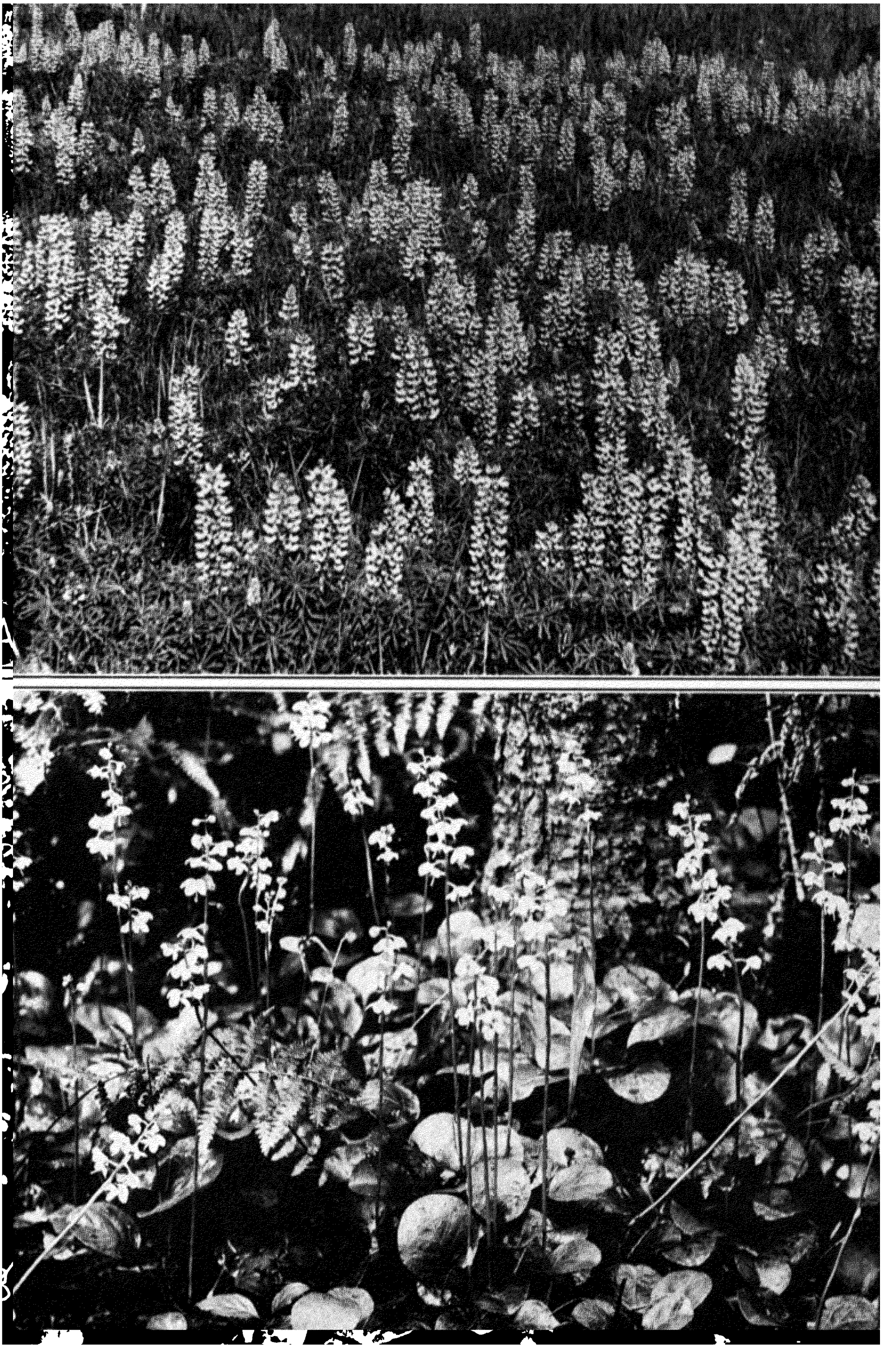
Aspect societies.—Since most societies are composed of subdominant herbs, *i. e.,* dominant within a dominance, their chief value usually appears as they approach maturity, and especially when they are in flower. *Astragalus crassicarpus,* for example, is present in the prairie from early spring to frost. But it dominates hillsides only in the spring, before the taller herbs have grown, and this dominance is a conspicuous feature only when the plants are in bloom. There is, then, a seasonal change of dominance which marks the

aspects of vegetation. In open woods a similar change of dominance results from the successive appearance of the layers, the earlier lower layers being masked by taller later ones. Thus there may be distinguished prevernal, vernal, æstival, and autumnal aspects, and corresponding societies. In boreal and alpine regions the number of aspects is often but two, vernal and æstival, and the societies correspond. The large majority of societies fall more or less clearly within one aspect, but there are exceptions, as previously suggested. Hence it is necessary to establish a major distinction into aspect societies and permanent societies. Many of the latter are not true societies at all, but are more or less imperfect expressions of undershrub and scrub consocies which represent a potential climax. Such are the *Gutierrezia, Yucca,* and *Artemisia cana* communities of the Great Plains.

Layer societies.—As already indicated, these usually have a seasonal relation also, as they tend to develop successively rather than simultaneously. The societies of thicket and woodland differ from those of grassland in being more coherent and in falling into well-marked layers. The latter are found in prairie, but they are usually incomplete and obscure. When the development of the layers is clearly seasonal, the societies concerned may well be regarded as aspect societies. As a rule, however, the layers are all developed before midsummer, and the forest presents a distinctively storied appearance. Naturally, the layers are often fragmentary or poorly defined, and in closed or mature forests they may be lacking. It seems best, then, to distinguish but two kinds of layer societies at present, namely, societies of the shrub layer or layers, and societies of the herbaceous layers. In cases where tall herb layers overtop one or more of the shrub layers this distinction has little value, but as a rule, the essential difference in the life-forms of the two layers or sets of layers marks a convenient if not an important distinction (*cf.* Hult, 1881).

Cryptogamic societies.—These in turn bear some relation to layer and seasonal societies. The lowermost layer of a thicket or forest often consists of mosses, liverworts, lichens, and other fungi. In mature forests of spruce this is often the sole layer. Nearly all the parasites and many of the saprophytes can not develop until stems and leaves appear, and hence exhibit both a seasonal and a layer relation. While there can be no question of the distinctness of cryptogamic societies, their treatment is a difficult matter. Many of them are actual colonies in minute seres, such as the pure or mixed communities of *Marchantia, Funaria,* or *Bryum* in burned spots. Distinctions into ground societies, parasitic societies (*i. e.*, those mostly on leaves and herbaceous stems, which necessarily disappear each season), and bark societies (which persist from one year to another) are convenient, but of minor importance. A distinction based upon life-form, *i. e.*, moss, liverwort, lichen, and fungus, is probably of greater value. Perhaps a more exact analysis would result from the use of both life-form and location, but such a basis produces results too detailed for our present needs. The soil in particular presents a virgin field for the recognition and limitation of parasitic and saprophytic societies and socies, especially of bacteria, but our knowledge is too slight to furnish the necessary criteria.

Terminology.—Societies have been designated by adding the locative suffix *-ile* to the name of the dominant genus, *e. g.*, *Iridile, Opulasterile, Androsacile* (Clements, 1905:299). Layers were named in similar fashion by



A. Lupine society, *Lupinus plattensis*, in mixed prairie, Hat Creek Basin, Nebraska.
B. Clan of *Pirola elliptica* in forest, Lake Calhoun, Minnesota.

adding *-anum* to the generic name or group, *Opulaster-Ribesanum.* Since the society is usually a group with a definite impress and a basic relation to habitat conditions, much as in the consociation, it seems appropriate that it should likewise bear a locative suffix. For these reasons the suffix *-ile* is retained to designate societies in general and aspect societies in particular. It may well serve also for thallophytic societies, *e. g., Funarile, Marchantile, Cladonile, Agaricile,* since the generic name clearly indicates the life-form. When it seems desirable to distinguish layer societies, it may likewise be done most simply and briefly by means of a suffix. Since the suffix *-anum,* already used for layer, is unnecessarily long, it is proposed to replace it by *-en, e. g., Fragarien, Thalictren, Erythronien, Helianthen.* Where mixed societies exist there is no better method than to combine the two generic names, *e. g., Psoralea-Helianthile.*

Changes of rank or dominance.—Since consociation and society are based chiefly upon dominance as controlled by habitat, it sometimes happens that the dominance changes to such a degree or over such an area that the community loses its usual rank. A consociation may appear to be a society, or even a clan. A society may assume the appearance of a consociation, or, on the other hand, may likewise be so reduced as to resemble a clan. Such changes in value occur most frequently (1) in or near transition areas, (2) as a result of temporary oscillations of climate, and (3) in the course of successional development, during which consociations may dwindle to insignificant groups, or colonies which appear to be societies or clans develop into consociations. The last is typically the case with such undershrubs as *Gutierrezia, Artemisia, Yucca,* etc., which often appear as clans and societies in grassland. These communities, however, are really the beginnings of a postclimax consociation, the full development of which is conditioned upon a climatic change.

It is possible to treat communities of this sort solely with reference to their actual value in a particular association, without regard to their normal or developmental relation. Such a method is simpler and more convenient, but it has the disadvantage of obscuring the organic relations and of confusing the facts of development. Consequently it is thought best to regard consociations and societies as entities, which may increase or decrease markedly in dominance and extent under certain conditions. However, if the facts are made clear, it matters little whether a particular group is called a reduced consociation or a society which represents a consociation of a contiguous area. Theoretically it is possible, at any rate, that a consociation of one region may be changed into a typical society in another.

Clan.—A clan is composed of a secondary species. It is next below the society in rank, though it is not necessarily a subdivision of it. Clans may and usually do occur in societies, but they are also found in consociations where there are no societies. A clan differs from a society chiefly in being local or restricted to a few small and scattered areas. Its dominance is slight or lacking, though it may often furnish a striking community in the vegetation. While societies and clans can usually be distinguished with readiness, there is no hard and fast line between them. Even the use of quadrat methods can not always distinguish them clearly. A clan differs from a colony in being a more or less permanent feature of climax communities or of consocies which exist for a long time. A colony is a group of two or more

species which develops in a bare area or in a community as an immediate consequence of invasion (plate 16 B).

Clans are distinguished upon the same bases as societies. They are connected for the most part with particular aspects, and the vast majority of them are aspect clans. The minor groups of layers are layer clans, and the clan may also be recognized in the moss, lichen, and fungus communities. The term *clan* is a partial synonym for *community* in the original sense (Clements, 1905: 297; 1907:227, 240). It comprises the communities found in subclimax and climax stages, while the invading or developing communities of initial groups are termed colonies. Communities have been designated by means of the suffix *-are* (*l. c.*, 1905:299), and it is now proposed to restrict the use of this suffix to the clan, *e. g., Gentianare, Mertensiare,* etc.

SERAL UNITS.

Nature and significance.—The units which have just been considered are essentially climax communities. In addition, there are similar or analogous communities throughout the course of succession. To many it will appear an unnecessary if not an unwelcome refinement to recognize a developmental series of units. To such students the series already established, viz., formation, association, consociation, society, and clan, will suffice for all units without regard to a distinction between developmental and climax phases of vegetation. However, for those ecologists who regard the formation as an complex organism, it is as essential to distinguish developmental and climax communities as to recognize gametophytic and sporophytic generations in the life-history of the individual.

The need of such a distinction has already been at least suggested by Hult (1885) and Klinge (1892) in their recognition of climax formations, and especially by Drude (1890:29; 1896:286) when he states that he "regards as a vegetation formation each independent closed chief association of one or several life-forms, whose permanent composition is effected by the definite conditions of the habitat, which keep it distinct from the adjacent formations." Schimper (1898) seems to have had some idea of this distinction in his recognition of climatic and edaphic formations, while Warming (1896: 361; 1909:356) and Clements (1902:15; 1904:134) also suggested it in distinguishing between initial, intermediate, and ultimate formations. Moss (1910:32), in this connection, says that:

"As a definition of a closed, ultimate or *chief* association of a formation, this statement of Drude's is excellent, though, as his 'formation' is essentially only a particular kind of association, it is not quite consistent with the views of those authors who regard the formation as related to the association as the genus is to the species. . . . From the point of view of succession, the formation of Drude, variously termed by him 'Formation,' 'Hauptformation,' and 'Hauptbestand,' must be regarded as a *chief* association of a formation. The chief associations of a district, however, do not comprise the whole of the vegetation of that district; they serve to give a vivid but somewhat impressionistic picture of such vegetation; and the complete picture requires the addition of the details provided by the progressive and retrogressive associations, or, as these may be collectively termed, the *subordinate associations.*" (37)

Moss (1910:36-38) further emphasizes the importance of distinguishing between climax and developmental associations:

"A plant formation, then, comprises the progressive associations which culminate in one or more stable or chief associations, and the retrogressive associations which result from the decay of the chief associations, as long as these changes occur in the same habitat. . . . The above examples of succession are given in order to show the importance of regarding the formation from the point of view of its developmental activities. . . . Every formation has at least one chief association; it may have more; and they may be regarded as equivalent to one another in their vegetational rank. They are more distinct and more fixed than progressive or retrogressive associations. They are usually, but not invariably, closed associations. They always represent the highest limit that can be attained in the particular formation in which they occur, a limit determined by the general life conditions of the formation."

Tansley (1911:12) has adopted the same view:

"Thus each of the types of vegetation, woodland, scrub, and grassland, *within a given formation,* is a plant association, and so is each definite phase in the primary development of a formation. The highest type of association within a formation (often woodland), to which development tends, is called the *chief association* of the formation. In the absence of disturbing factors, such as the interference of man, land-slips, and so on, the chief associations will ultimately occupy the natural formation area to the exclusion of the other associations, which may collectively be termed *subordinate associations.*"

Cowles (1910) has also recognized the essential difference between developmental and final communities, in using the term "climatic formation," which Moss (1910:38) points out is equivalent to his chief association. Moss regards Cowles's term as unfortunate, because it is used in a very different sense from the same term of Schimper. This is hardly the case, for while Schimper's term covers more than one kind of unit, the recognition of climatic and edaphic formations seems clearly to have taken some account at least of development. (*Cf.* Skottsberg (1910:5) and Vestal (1914:383).)

In spite of differences in their views of the formation, the nine authors just quoted, Hult, Klinge, Drude, Warming, Schimper, Clements, Moss, Cowles, and Tansley, have all distinguished more or less clearly between climax and developmental associations. Such a distinction naturally does not end with associations, but extends throughout the units. Hence it is here proposed to recognize and define a series of developmental units in the life-history of the climax formation, which is essentially analogous with association, consociation, society, and clan. In fact, a failure to do this causes us to ignore practically all the developmental study of the past 20 years, and to make the developmental analysis of vegetation difficult and confusing, if not impossible.

Associes.—The associes is the developmental equivalent of the association. It corresponds to the initial and intermediate formations of Clements (1902, 1904) and to the subordinate associations of Moss (1910) and Tansley (1911). It is composed of two or more consocies, *i. e.,* developmental consociations, just as the association consists of two or more consociations. Like the association, it is based upon life-form, floristic composition, and habitat, but differs

from it in as much as all of these are undergoing constant or recurrent developmental changes. In so far as each sere is concerned, the associes is transient, though it may persist for many years, and the association is permanent. Obviously, a medial or final associes may become an association when the development is held indefinitely in a subclimax stage, as in heath and prairie. On the other hand, a change of climate which advances the climax converts the previous associations into developmental units, and they thus become associes. This potential relation between association and associes naturally obtains wherever climax associations are zoned. This is especially evident in mountain regions, where grassland and scrub associations are potential associes of the forest above (plate 17 A).

In its complete expression, the associes is marked by striking changes of both habitat and life-form, as necessarily of floristic. This is best illustrated in water seres, the initial stages of which constitute three well-marked associes, namely, submerged plants, floating plans, and swamp plants. In each there is a pronounced change of habitat necessarily accompanied by a corresponding change of life-form and floristic. While it seems probable that all important changes of life-form are due to the reaction upon the habitat, certainty in this respect is impossible as yet. It can be attained only by the instrumental study of conditions before and after the change of life-form. Theoretically, such a relation seems highly probable, and we may assume as a working hypothesis that one associes is delimited from another by important changes of habitat, as well as life-form. In the prisere of the spruce-fir formation, for example, it is probable that the change from crustose to foliose lichens is as great a change of habitat as happens anywhere in the sere, but it is too minute in extent to be impressive.

While associes is obviously from the same root as association, it is based upon the original meaning of sequence (*sec-*, *soc-*, follow) rather than the derived one of companionship. Though the form *assecies* is preferable for some reasons, it is less euphonic and less suggestive of the relation of association. It seems desirable to emphasize the relationship between the two units by terms evidently related rather than to employ a wholly new word. For the same reason the names of particular associes are based upon the words already used for formation and association. These three units have so much in common that the same root modified by a different suffix seems to harmonize readily with the actual degree of similarity and difference. For associes, the termination *-is* is proposed, and we would thus have *helis, pois, hylis, eremis,* etc., *e. g., Scirpus-Typha-helis, Andropogon-Aristida-pois,* etc.

Consocies.—The consocies is a seral community marked by the striking or complete dominance of one species, belonging of course to the life-form typical of that stage of development. It is the unit of the associes in the same way that the consociation is of the association. The consocies and consociation differ only in that the former is a developmental or seral, the latter a climax, community. *Bouteloua* and *Bulbilis* are consociations of a climax association of the Great Plains, *Andropogon scoparius* and *Aristida purpurea* are consocies of a seral association, or associes. Because of its developmental nature, the reed-swamp association is an associes in the present conception, and each of its dominants, *Scirpus, Typha, Phragmites,* etc., forms a conso-

A. Grass associes of *Andropogon* and *Calamovilfa*, Crawford, Nebraska.
B. *Pentstemon* socies (*P. secundiflorus*) in gravel, Manitou, Colorado.

cies. The heath association is likewise an associes, except where it may have been stabilized to form a climax, and *Calluna* and *Erica* form the characteristic consocies of it.

The term consocies likewise is obviously related to consociation. In the latter, however, the suffix emphasizes the condition of being grouped together. In consocies, on the contrary, the emphasis lies upon the root *seq-* (*sec-, soc-*) found in *sequor,* and denoting sequence. This may be illustrated by the case of the reed-swamp consocies. As is well known, the three dominants are not exactly equivalent, but *Scirpus* usually invades the deepest water and *Phragmites* the shallowest, so that the corresponding consocies show a definite sequence, even though they are all present at the same time. Such a successional relation is typical of the dominants of an associes, and it is just this relation which is denoted by the name consocies. It must also be recognized that an associes may be represented in one locality by only one of two or more consocies; for example, *Typha* may alone represent the three usual consocies of the reed-swamp. Particular consocies may be indicated by using a suffix with the generic name, as in the case of consociation. It is proposed to employ the suffiix *-ies* for this purpose, as in *Scirpies, Typhies, Phragmities, Aristidies,* etc.

Socies.—The socies bears exactly the same relation to consocies and associes that the society does to consociation and association. It is a seral society, characteristic of a developmental community instead of a climax one. It is marked by subdominance within the dominance, in the way that a society is composed of a subdominance within a climax dominance (plate 17 B).

Socies show the same differences as those found in societies. They are more or less characteristic of aspects, and they occur in layers, though to a smaller extent, since layers are well-developed only in the final stages of a sere. Cryptogamic or thallus socies are especially numerous, since such communities are characteristic of many initial stages. As is evident, the term socies comes from the root *seq-* (*sec-, soc-*), *follow,* found in its primary or secondary meaning in all the preceding terms. While the prefix *con-* in consocies indicates the grouping of seral dominants to form an associes, its absence in socies suggests the fact that the latter are not exact subdivisions of the consocies. Socies are designated by using the generic name with an affix, as in the case of the society. In place of the locative suffix, *-ile,* the diminutive *-ule* is proposed, as in *Sedule, Violule, Silenule,* etc. This has the advantages of at least suggesting the earlier seral position of the socies with reference to the society, and of indicating by the similarity of the two suffixes the close relationship between the respective communities.

Colony.—The colony is an initial community of two or more species. It is practically always a direct consequence of invasion, and hence is characteristic of the early seral development in bare areas. It may arise from the simultaneous entrance of two or more species into the same spot, or it may result from the mingling of families. From their occurrence in bare areas, particular colonies are nearly always sharply delimited. They may appear in the midst of later dense communities whenever a minute bare spot permits invasion, or whenever success in competition enables an invader to make a place for itself. In such places they simulate clans, but can be readily distinguished by a careful scrutiny.

Colonies resemble clans in their usually limited size and in the absence of a clear relation to the habitat, because they are still in the process of invasion. They differ in appearing normally in bare areas or in open vegetation and in being developmental in character. A colony differs from a family in consisting of two or more invaders instead of one. It is one of the two kinds of community formerly recognized by Clements (1905:297; 1907:227, 239). A colony does not have a fixed rank, but it may develop later into any community of higher rank in the developmental series. As already indicated, it is primarily a mixed invasion group, which is inevitably worked into the history of the sere as development proceeds. The term *colony* is itself an index of this pioneering quality. Colonies may be designated by the suffix *-ale*, as in *Hordeale, Ambrosia-Ivale*, etc.

Family.—The use of the term *family* for an ecological group was proposed by Clements (1904:297, 299; 1905:297; 1907:228, 237). The fundamental identity of such families of plants with those of animals and man is thought to make such use of the word unavoidable in spite of the established usage for a systematic unit. While the possibility of confusion from the double use of the term is slight, it may prove desirable to avoid this objection altogether by using the term *famile* for the ecological unit. As is evident, it is from the same root as family, and has essentially the same meaning.

A family is a group of individuals belonging to one species. It often springs from a single parent plant, but this is not necessarily the case, any more than in a human family. It may consist of a few individuals or may extend over a large area. The group of cells within a *Gloeocapsa* sheath is a family, and not a colony in the proper sense. The coating of *Pleurococcus* on a tree-trunk is a family, as is also a tuft of *Funaria* at its base, or the group of *Helianthus* which fills a large field to the exclusion of all other flowering plants. Families, however, are usually small, since they are more readily invaded when large, and consequently pass into colonies. They are especially typical of bare areas and initial stages. They rarely appear in dense vegetation, except where local denudation occurs. As the individuals of a family become more numerous, adjacent families merge into a colony; or migrules from one family may invade another at some distance and convert it into a colony. Since the family always consists of a single species, it may be designated in the usual way by adding the patronymic suffix to the generic name, as in *Sedas, Aletas, Eriogonas*, etc. Where greater definiteness is desired, the specific name in the genitive form may be added, *e. g., Rubas strigosi*.

Summary of units.—The following table is intended to show the relation of climax and seral or developmental units to the formation, the relation of the units of each series to each other, and the correspondence of units in the two series.

FORMATION.

Climax Units:	Seral Units:
Association	Associes.
Consociation	Consocies.
Society	Socies.
Clan	Colony.
	Family.

Mixed communities.—Clements (1905:304; 1907:235) has considered briefly the mixing of communities as a consequence of juxtaposition or of

A. *Artemisia-Populus-ecotone*, Fallon, Nevada.
B. *Picea-Populus-mictium*, Alpine Laboratory, Colorado.

succession. The former applies to the characteristic mingling of dominants where their corresponding communities touch. It may occur between two or more formations, associations, consociations, or societies, or between associes, consocies, or socies. In every case the mixing takes place at the borders of the communities concerned, producing an ecotone or tension. This is often very extensive, and frequently its relations are very puzzling. Difficult as the task may be, however, the real nature and significance of such an ecotone can be determined only from a study of the adjacent communities.

The mixing of two stages in development is much more complex and puzzling. This is due to the fact that mixing may take place throughout the area and in varying degree. There are consequently in such places no distinct areas of the two stages with which comparison can be made. Hence it is necessary to turn to other examples of the same development and to make a comparative study extending over a wide region and over several years. While there is inevitably some mixture in all stages of the sere, it is only when the dominant species of two, or rarely more, stages are present on somewhat of an equality that a real mixture may be said to result. It is now proposed to restrict the term *mictium* (Clements, *l. c.*) to this developmental mixture, and to use *ecotone* for an actual transition area on the ground between two communities, regardless of whether the latter are climax or seral. Thus, a *Populus-Pinus-mictium* is a more or less uniform mixture of two successive consocies, while a *Populus-Pinus-ecotone* is a band of mixed aspen and pine between two pure communities of each (plate 18, A, B).

Nomenclature of units.—The whole task of ecological nomenclature is to secure a maximum of characteristic with the minimum effort. A long step toward this result is taken by having a definite concept and name for every distinct unit. The method of suffixes, first used by Schouw (1823:65) in designating groups by adding *-etum* to the generic name, has furnished the model for the designation of all groups in which life-form and dominance are the chief characteristics. Such are the consociation, consocies, society, etc. Where the habitat is of primary importance, as in the formation, association, and associes, it is necessary to employ a separate word, *poion, helion, hylion, eremion,* etc., to indicate it. This must then be qualified by the use of the generic name for actual floristic definiteness (Clements, 1902:16). Difficulties arise, however, when two or more genera are concerned, or when it is necessary to indicate the species in order to secure the requisite definiteness. In both cases a balance must be struck between usability and definiteness, and the latter must often be sacrificed. In the case of the Great Plains grassland, definiteness would demand that it be termed the *Bouteloua-Bulbilis-Aristida-poion.* Such a name is impracticable, as taxonomy long ago proved in the case of polynomials. The use of two generic names is the most that convenience permits, and one is better still. In the case cited, since *Bouteloua* is the dominant of the widest range and greatest importance, the grassland might well be called the *Bouteloua-poion.* Once the names of units become generally recognized, such a designation is no more indefinite or incomplete than Solanaceæ, for example.

In this connection, Moss (1910:41) states that:

"The naming of a pure association [consociation] by its dominant species is comparable with the plan of naming a systematic group after an easily

recognizable character; and in neither case does such a name exhaust the characters of the group it denotes."

This statement does not seem wholly consistent with the further statement that:

"This name, *Eriophorum-Scirpus-Oxodion,* would not, however, be really definitive, as no indication would be given of the species of *Eriophorum* or *Scirpus,* which are the dominant plants of the two associations; and the range of habitat and of form of these two genera is considerable. Nor do such terms as 'magna-Caricetum' and 'parvo-Caricetum' (Schröter, 1904:49) overcome this difficulty in the least. In the British Isles alone there are, in this formation, associations of *Calluna vulgaris,* of *Empetrum nigrum,* of *Eriophorum angustifolium,* of *E. vaginatum,* of *Molinia coerulea,* of *Vaccinium myrtillus.* and others. Add to these the various other associations known and described on the continent of Europe alone, and the designation of the formation by Clements' plan reaches Brobdingnagian proportions."

While no such sesquipedalian terms were contemplated in the plan mentioned, the criticism loses its weight in the case of the developmental classification of formations as climax units. Each formation would rarely contain more than two or three associations, and it is merely a question of a compromise between securing the necessary brevity and the desired definiteness. Where the generic names of the chief dominant of each association are short, two or three such names might be used with maximum definiteness and little inconvenience. As a rule, however, two names alone would be permitted by the demands for brevity, and often one would be better still. Once in use, *Bouteloua-poion, Stipa-poion,* or *Picea-hylion* would be no more indefinite than Solanaceae, Rosaceae, etc. It seems such a designation of the formation would have a distinct advantage over the proposal to designate the various climatic formations as α-Oxodion, β-Oxodion, etc. (Moss, 1910:44). In the case of mixed communities, definiteness demands the use of the two chief dominants, whether they are consociations as in an ecotone or consocies as in a mictium.

Hult (1881:22) was the first to propose and use a system of nomenclature for formations. He considered the use of names based upon the habitat to be impossible, for the reason that the same formation [community] might occur in quite different habitats. Hence he found it necessary to propose an entirely new nomenclature, modeled after Kerner, in which formations were named from their characteristic vegetation-forms. As he understood it, the pine formations contained three such forms, the *Pinus*-form, *Myrtus*-form, and *Cladina*-form, and hence were termed "pine and lichen formations," *Pineta cladinosa.* Hult's evident intention was to form a binomial nomenclature based upon that of taxonomy, an attempt which has much to commend it theoretically. Practically it results too often in a lack of definiteness and brevity, produces an endless series of names, and fails completely to indicate developmental relations. Such names as *Pineta cladinosa, Betuleta muscosa,* and *Aireta geraniosa* are attractive, but *Geranieta graminifera, Aireta herbida* and *Aireta pura* are ambiguous and confusing, while *Sphagneta schoenolagurosa, Juncelleta polytrichosa, Pseudojunceta amblystegiosa,* and *Grandicariceta amblystegiosa* are quite too long and indefinite.

Cajander (1903:23) has proposed to designate associations (consociations) more exactly by using the genitive of the species with the generic name in

-etum, e. g., Salicetum Salicis viminalis, though in use this becomes *Salicetum viminalis, Alnetum incanae,* etc. Moss (1910:41) adopts this plan, and Warming (1909:145) apparently approves it also. As a consequence, it may well be generally adopted in all cases where such definiteness is desired. In the actual consideration of a consocies or other unit it would seem unnecessary and inconvenient to repeat the full form, *e. g., oxodion Eriophoreti vaginati, Aristidae purpureae pois,* etc. The full form once given, *Eriophorum-oxodion* or *Aristida-pois* would meet all requirements, except where actual confusion may arise when there are two dominants of the same species in one association or associes.

The names of units are necessarily long at best, and it seems both desirable and justifiable to shorten them in every legitimate way. The most efficient way of doing this is the one already suggested, namely, of using the name of the chief genus or even a characteristic genus alone in the case of formation, association and associes, exactly as has been found so successful in the case of families and orders. In the case of terminations in particular there can be no valid objection to the use of shortened stems and of the contraction or elision of successive vowels. The classical purist will find the former method objectionable, but the fact remains that it was in use by classical writers themselves. A study (Clements, 1902:31) of Greek neuters in -ματος, nom. -μα, *e. g., sperma, stoma,* etc., has shown that some of them occur usually in this form, and still more take this form frequently. In their use in biology, Greek and Latin must be regarded as living languages and hence subject to change along the lines already indicated. Hence there is the warrant of brevity and convenience as well as of actual classical practice for the shortened forms found in *Spermophyta, Dermocybe, stomal,* etc. This usage may well be extended to other imparisyllabic stems in *-idis, -itis,* etc. Thus *Calamagrostidetum* would become *Calamagrostetum; Heleocharitetum, Heleocharetum; Lychnidetum, Lychnetum.* Such abbreviations have already been made, though it is very doubtful whether such extreme cases as the shortening of *Potamogetonetum* to *Potametum* are to be approved. The contraction or elision of vowels especially is often desirable also, even though the gain is small. The chief gain is in pronunciation rather than in spelling as *Picetum* for *Piceetum, Hordetum* for *Hordeetum,* and *Spiretum* for *Spiraeetum.*

Formation groups.—The arrangement of formations into higher groups has been based upon various grounds. The first systematic grouping was that of Schouw (1823:157), who used the amount and nature of the water-content to establish the four generally accepted groups *hydrophyta, mesophyta, xerophyta* and *halophyta,* though he named only the first and last. The term *xerophyte* or *xerophilous* dates back to Thurmann (1849) and *mesophyte* to Warming (1895), who adopted Schouw's classification in essence. Drude (1890:37) classified formations as (1) forest, (2) grassland, (3) swamp moor, (4) miscellanous, rock, water, and saline. Pound and Clements (1898: 94; 1900:169) adopted Warming's divisions, but subdivided mesophytes into *hylophytes, poophytes,* and *aletophytes.* Schimper (1898), while recognizing water-content groups, classified formations with respect to life-form as forest, grassland, and desert, and with regard to habitat as climatic and edaphic. Graebner (1901:25) grouped formations on the basis of soil solutes into those

on (1) pernutrient, (2) enutrient, (3) saline soils. Cowles (1901:86) used physiography and development for the basis of the following groups: (A) Inland group: (1) river series, (2) pond-swamp-prairie series, (3) upland series; (B) Coastal group: (1) lake-bluff series, (2) beach-dune-sandhill series. Clements (1902:13) arranged formations in various groups, based upon medium, temperature, water-content, light, soil, physiography, physiognomy, association, and development. Schröter (1902:73) proposed two major groups: (1) vegetation type, subdivided into (2) formation groups, and the latter into formations. Grassland is given as an illustration of the vegetation type, and meadow of the formation group. Clements (1904:139; 1905:302, 270) arranged formations with reference to habitat, development, and region, but emphasized the developmental classification as primary. Warming and Vahl (1909:136) propose 13 classes of formations on the basis of climatic and edaphic distinctions. To the original 4 groups of Warming are added *helophytes, oxylophytes, psychrophytes, lithophytes, psammophytes, chersophytes, eremophytes, psilophytes, sclerophyllous,* and *coniferous* plants (*cf.* Clements, 1902:5). Brockmann and Rübel (1913:23) have recognized three major groups: (1) vegetation type, (2) formation class, and (3) formation group. For example, the vegetation type, woodland or "Lignosa," is divided into several formation classes, *e. g.,* "Pluviilignosa," "Deciduilignosa," etc., and these into groups, such as "Aestatisilvae," "Aestatifruticeta," etc. The primary basis of the classification is physiognomy, with some reference to habitat in many of the classes and groups.

Bases.—A comparison of the various systems proposed above shows that there are three general bases. These are habitat, physiognomy, and development. These practically exhaust the list of possibilities, since floristic does not furnish a feasible basis. All systems based primarily upon habitat make use of physiognomy in some degree, and the converse is also true. They do not take development into account, and hence are more or less superficial. The simplicity and convenience of artificial classifications based upon habitat and physiognomy are so great, and the readiness with which they can be made is so alluring, that they will persist for a long time. They must slowly yield to a natural system based upon development, but such a system in its details demands much more knowledge of vegetation and climate than we possess at present. There can be no serious objection to using a habitat-physiognomy or a physiognomy-habitat system in so far as it is useful and accords with the facts. It should be constantly borne in mind, however, that such classifications are makeshifts against the time when developmental studies have become general.

Developmental groups.—The formation as generally understood is based in no wise upon development. Hence the natural or developmental relation of such formations or associes, as they are called here, is revealed by the physiographic classifications of Cowles (1901). Such a system broadened to become purely developmental, and with physiography regarded as but one of several causes is the one which we have already considered in various aspects. The formation as here conceived is a natural unit in which all of its associes, the formations of many authors, fall into their proper developmental relation. It has already been pointed out that such a relation includes all the essentials of habitat and physiognomy.

The classification of formations, *i. e.*, climax communities, as here understood, is a more difficult task. Here again the fundamental basis should be that of development, but we now have to do with the phylogenetic development of a climax formation, and not with its ontogeny. The ontogenetic development of a formation, such as the Great Plains grassland, can be studied in hundreds of primary and secondary seres. Its phylogeny is a matter of the past. It not only can not be studied with profit until the present development is well understood, but it must always remain partly a matter of speculation. It is only in the case of fairly complete records, such as those of peat-bogs, that the actual origin of a climax formation can be traced. From their very nature such formations are dependent upon climate. This fact furnishes the best basis for a natural classification at present. In this connection it is instructive and convenient to group the climaxes of similar climates together, as for, example, the plains of America and the steppes of Eurasia. Such a classification emphasizes the essential relation of climax and climate, but is not necessarily genetic. Such a genetic or developmental classification can be based at present only upon the regional relation of climaxes, as indicated in Chapter IX. A system of this sort is suggested by the regional classification of Clements (1905:304), in which (1) lowland, (2) midland, (3) upland, (4) foot-hill, (5) subalpine, (6) alpine, and (7) niveal formations correspond closely to a similar series of climaxes, namely, (1) deciduous forest, (2) prairie, (3) plains, (4) scrub, (5) montane forest, (6) alpine grassland, (7) lichen and moss tundra. A similar relation exists in the case of continental zones of temperature (*l. c.*, 283), the (1) polar-niveal, (2) arctic-alpine, (3) boreal-subalpine, (4) temperate, (5) subtropical, and (6) tropical zones, corresponding essentially to as many climatic climaxes, more or less interrupted by the superimposed series indicated above.

The sequence of climates and climaxes in either of the above series indicates the course of development in the event of any normal climatic change. If the climate of the Mississippi basin becomes drier, prairie will encroach upon and replace deciduous forest, and the plains will conquer prairie to the east and scrub to the west, etc. If the rainfall increases the deciduous forest will extend more and more into the prairie, the latter will move westward over the plains, and the plains will be further narrowed by the creeping out of scrub and forest from foot-hills and mountains. The appearance of another period of glaciation would produce a similar shifting of climaxes. The polar-niveal climax would move into the arctic-alpine climax, the latter into the boreal-subalpine climax, etc., the amount of movement and replacement depending upon the extent and duration of the ice. The reverse migration of climaxes would occur upon the melting of the ice-sheet, as it must have occurred at the end of the glacial epoch, and to a certain extent in interglacial intervals. A climatic series of climaxes or formations is an epitome of past and potential development, *i. e.*, of phylogeny. It is both genetic and natural, and furnishes the basis for a natural classification of climax formations. Such a series is the connecting link between the coseres of one climatic period and another, that is, between two different vegetation periods geologically speaking, or eoseres. From its step-like nature and its relation to climate and climax, such a regional-historical series may be termed a *clisere*. This term is formed

by combining sere with the unmodified root *cli,* found in Gr. κλίνω, make to bend or slope, κλίμα, slope, region, climate, and Lat. *clivus,* slope, hill. In accordance with what has been said above, it is here proposed to group formations in climatic series or cliseres. The illustrations already given would constitute two cliseres, one dependent upon water primarily, the other upon temperature. Cliseres in turn would be related to definite eoseres.

VIII. DIRECTION OF DEVELOPMENT.

Development always progressive.—Succession is inherently and inevitably progressive. As a developmental process, it proceeds as certainly from bare area to climax as does the individual from seed to mature plant. While the course of development may be interrupted or deflected, while it may be slowed or hastened, or even stayed for a long period, whenever movement does occur it is always in the direction of the climax. In this connection, however, it is imperative to distinguish between the development of the sere and the action of denuding agencies. This is particularly necessary when such a process as erosion acts with varying intensity in different portions of the same area. At first thought it seems permissible to speak of such a community as degenerating or retrograding. A closer analysis shows, however, that this is both inaccurate and misleading. What actually occurs is that the community is being destroyed in various degrees, and secondary areas of varying character are being produced. In these, colonies appear and give a superficial appearance of regression, but in no case does actual regression occur. In every denuded area, no matter how small, development begins anew at the stage determined by the degree of denudation, and this development, as always, progresses from the initial colonies to or toward the climax formation.

Nature of regression.—Regression, an actual development backwards, is just as impossible for a sere as it is for a plant. It is conceivable that lumbering, grazing, and fire might cooperate to produce artificial regression, but there is nowhere evidence that this is the case. Apparent regression would, and probably does, occur when the forest canopy is removed by the ax and the shrub layer is also later removed as a consequence of grazing or fire, permitting the final establishment of herbland or grassland. Here, however, there can be no question of development, for the whole process is one of destruction, of partial denudation. The consocies resemble those of the final stages of the original sere, but are largely or wholly different as to the constituent species. The actual condition is one characterized by the removal of the dominants and the consequent change of the controlling conditions. The latter results in the disappearance of many principal and secondary species and the concomitant invasion of new ones. As long as the artificial forces which brought this about persist or recur, the community will be held in a subclimax, *i. e.*, the development is checked in much the same way that extreme cold or wet stops the growth of the individual plant. Once the inhibiting forces are removed, normal development is slowly resumed and progresses to the proper climax, provided the climax community still persists in adjacent areas.

The apparent exception afforded by the *Sphagnum* invasion of grassland or woodland communities is discussed a little later. Here again a close scrutiny of the facts indicates that this is but another case of local and partial denudation due to water. The case is complicated by the fact that the growth of *Sphagnum* is both a cause and a consequence of the increased water and of the resulting denudation by overwhelming or flooding. Successionally, *Sphagnum* stands in the same causal relation to the flooding that a beaver-

dam or local surface erosion does. It is both a cause and a pioneer, however, and this dual rôle has tended to conceal the essential relation.

Course of development.—The basic and universal progression from bare areas to climax is a complex correlated development of habitat, community, and reaction. The general relation of these is indicated by the gradual colonization of a bare area, and the progression of associes until the climax is reached. Beneath this, as motive forces, lie invasion and reaction. The total effect is seen in four progressive changes or processes. The initial change occurs in the habitat, which progresses normally from an extreme or relatively extreme condition to a better or an optimum condition. This is especially true of the unfavorable extremes of water-content, both as to quantity and quality, *i. e.*, the presence of alkali, acid, etc. With respect to the plant life, the progressive movement is from lower to higher phyads, from algæ, lichens, or mosses, to grasses and woody plants. The interaction of habitat and community results in a progressive increase of dominance and reaction, both in the most intimate correlation. Finally, in the climax formation as a whole, there is the simultaneous progression of almost innumerable primary and secondary seres, all converging toward the climax into which they merge.

Regression and retrogression.—It has already been stated that regressive development is impossible and that regressive succession does not occur. Hence it becomes necessary to examine the views of several authors who distinguished between progressive and regressive succession and to interpret their observations in terms of development. Such a distinction seems first to have been made by Nilsson (1899) in the study of the development of Swedish associations. Cowles (1901) used the same terms, but with a very different meaning, in his physiographic treatment of the ecology of the region about Chicago. Cajander (1904) adopts the distinction proposed by Nilsson, as does Moss also (1910), while Hole (1911) uses progressive and regressive in still another sense. As will become evident, some of these concepts are subjective and have little relation to the organic development, while others rest upon an incomplete interpretation of the facts. The existence of five conflicting views seems to afford illuminating evidence as to the actual occurrence of such a distinction in nature.

Nilsson's view.—The regular development of vegetation about the lakes of Sweden exhibits the following stages: (1) sedge moor; (2) *Eriophorum* moor; (3) scrub moor, with various consocies, chiefly *Calluna*, *Erica* and *Betula;* (4) forest moor, usually *Pinus silvestris*, often *Picea* or *Betula*. This is properly regarded as progressive development. Regressive development is said to take place when lichens, *Cladina* and *Cladonia*, appear in the *Sphagnum* masses of the scrub moor, and come to play the dominant rôle, as the *Sphagnum* and shrubs die off in large measure. *Sphagnum*, *Eriophorum*, and the shrubs still persist, however, in scattered alternes. The cause of the regression lies in the drying-out of the upper layer, the death of the *Sphagnum*, and the consequent weathering of the peat. During wet seasons the lichens perish through the accumulation of water. *Eriophorum* and *Andromeda* persist longer, but finally die out also as a result of the continued accumulation of water. The water is colonized by *Sphagnum* and sedges, especially *Carex limosa*, *Scirpus caespitosus* or *Scheuchzeria*, and progressive development begins anew, to terminate in forest moor or to be again inter-

rupted by unfavorable conditions. This continues until progressive development prevails throughout the entire area, and finally terminates in the climax forest. The development rarely proceeds uniformly over a large area, but progressive and regressive areas alternate with each other constantly. (371)

Nilsson's whole description agrees perfectly with the course of events in a sere where local conditions bring about the destruction of a particular stage in alternating spots. He makes it clear that drying-out kills the *Sphagnum*, *Eriophorum*, and shrubs in certain areas, and produces conditions in which lichens thrive. In turn, the accumulation of water kills the lichens, and, more slowly, the relict *Eriophorum* and shrubs, and prepares a new area for the invasion of *Sphagnum* and sedges. In all of this destruction there is nothing whatever of an organic successional development. Wherever plants are destroyed, whether quickly or slowly, over large areas or in a spot of a few square centimeters, invasion becomes possible, and local development begins. A general view of a moor with alternating pools and hummocks, of drier and wetter places, may well give the appearance of regression. But this is an appearance only, for in each pool and on every hummock development proceeds always in a progressive direction, though it may be interrupted again and again by a change of conditions. Nilsson also regards the repeated passage from progressive to regressive to progressive again as indicating a circulation or cycle of development, but this view depends upon the existence of an actual backward development.

Cowles's view.—Cowles distinguishes between progressive and retrogressive succession chiefly upon physiographic grounds. The distinction is drawn clearly in the following statement:

"Retrogressive phases, *i. e.*, away from the mesophytic and toward the hydrophytic or xerophytic, must be included, as well as progressive phases away from the hydrophytic and toward the mesophytic." (81)

The distinction is further elaborated as follows:

"In flood plains, the meanderings of the river may cause retrogressions to the hydrophytic condition, such as are seen in oxbow lakes, or the river may lower its bed and the mesophytic flood plain become a xerophytic terrace. The retrogressive phases are relatively ephemeral, while the progressive phases often take long periods of time for their full development, especially in their later stages. . . . If a climate grows colder or more arid, we find retrogressive tendencies toward the xerophytic condition, while in a climate that is getting more moist or more genial, the mesophytic tendencies of the erosive processes are accelerated. . . . (82) Retrogression is almost sure to come in connection with terrace formation. A river may swing quite across its flood plain, destroying all that it has built, including the mesophytic forest. Not only is the vegetation destroyed directly but also indirectly, since the lowering of the river causes the banks to become more xerophytic. . . . (107) The life history of a river shows retrogression at many points, but the progressions outnumber the retrogressions. Thus a river system, viewed as a whole, is progressive. . . . (108) A young topography is rich in xerophytic hills and in hydrophytic lakes and swamps. There may be local retrogressions toward xerophytic or even hydrophytic plant societies, forming eddies, as it were, but the great movement is ever progressive and toward the mesophytic condition. So far as plants are concerned, however, a physiographic termi-

nology may be still used, since all possible crustal changes are either toward or away from the mesophytic, *i. e.*, progressive or retrogressive." (178)

In connection with succession on dunes, Cowles states that:

"A slight change in the physical conditions may bring about the rejuvenation of the coniferous dunes, because of their exposed situation. This rejuvenation commonly begins with the formation of a wind sweep, and the vegetation on either hand is forced to succumb to sand-blast action and gravity." (174)

Elsewhere (172) the dune complex is described "as a restless maze, advancing as a whole in one direction, but with individual portions advancing in all directions. It shows all stages of dune development and is forever changing." Such destruction of existing communities and the production of a bare area are essentially the same as the changes in moor which Nilsson calls regressive. Cowles nowhere applies this term to the dune sere, and appears in no place to speak of the succession or development as retrogressive. Indeed, the use of the word "rejuvenation" in this connection is a fortunate one, as it emphasizes the essentially reproductive nature of the developmental process.

The use of progressive and retrogressive in connection with the development of seres in river valleys illustrates the undesirability of transferring physiographic terms to the organic development of vegetation. It is evident that a river system shows almost constant, though more or less local retrogression throughout its general progressive development during a single cycle of erosion. The bed of a river, its banks, flood-plain, and terraces are constantly reshaped by erosion and deposition in conformity with a general law. The material of the land is not destroyed, but merely shifted. Such is not the case with the community which occupies an area of erosion or deposit. As shown above, Cowles points out in such cases that the vegetation is destroyed directly or indirectly. Hence there can be no such thing as retrogression in the successional development. What does occur is the universal phenomenon of succession, in which one seral development is stopped by the destruction of a particular stage, and a new sere starts on the bare area thus produced. If the term "retrogressive phase" be applied solely to the usually brief period when the community is being destroyed, it fits the facts, but is still misleading. It implies a backward development or devolution comparable to the progressive evolution or development of the sere, while as a matter of fact it applies not to development but to its complete absence, *i. e.*, to destruction (*cf.* Crampton, 1911:27; Crampton and MacGregor, 1913:180).

The difficulty of distinguishing progression as movement toward a mesophytic mean and retrogression as movement away from it is well illustrated in succession in desert regions. The development of vegetation in a desert lake or pond passes from hydrophytic to mesophytic, and then to xerophytic or halophytic stages. Organically this is a unit development from a bare area to a climax community. Yet the distinction just mentioned would require that it be divided into progression and retrogression. The only possible retrogression is in the decreasing water-content, and yet this decrease of water-content is a constant feature of the progression from ordinary water areas to mesophytic conditions. Similarly, the successional development along the coast of the Philippines would present a peculiar difficulty, if Whitford's interpretation is correct (1906:679). He regards hydrophytic forest as the climax, and the entire development would consequently be retrogressive.

In a later paper (1911:170), Cowles appears indeed to regard retrogression as little if at all different from destruction, and to interpret physiographic processes chiefly in terms of destruction and development or progression.

"As might be expected, the influence of erosion generally is destructive to vegetation, or at least retrogressive (*i. e.*, tending to cause departure from the mesophytic), while the influence of deposition is constructive or progressive (*i. e.*, tending to cause an approach to the mesophytic). On a somewhat rapidly eroding clay cliff of Lake Michigan . . . a marked increase in erosive intensity would destroy all vegetation, and a marked decrease in erosive intensity might institute a progressive vegetative succession. Frequently a growing dune is inhabited by xerophytic annuals and by a few shrubs or trees; such a place illustrates the extreme of topographic dynamics, but often the vegetation is static. A great increase in depositional intensity results in the destruction of all the plants, while a decrease in depositional intensity results in progressive succession."

Cajander's view.—Cajander (1904) has studied three moors of northern Finland in connection with Nilsson's concept of progressive and regressive development, and has reached the conclusion that these views are correct. Moor I is regarded as in the course of primary progressive development characterized by a continuous fresh green moss layer, with low and indefinite cushions of heath-moor. Moor II is assumed to be chiefly in regressive development, as it is made up of areas of cyperaceous moor separated by strips of heath-moor. The reasons for this view are that (1) many areas are bare spots of decayed turf, (2) the sedge areas are often sharply delimited and raised above the heath-moor areas, (3) the moss-layer is lacking or consists of other mosses than *Sphagnum*. In the extensive Moor III, regressive development has everywhere taken place, and cyperaceous communities occur throughout. In a large part of the moor the regressive development is followed by a secondary progressive development, and in small areas of the latter is found a secondary regressive development. On these grounds the author regards the view of Nilsson that there is a "circulation" or cycle in the development as well-grounded. As already pointed out in this connection, regressive development is only destruction or denudation followed by the normal development, which is always and inevitably progressive. Denudation or destruction may recur again and again at any stage of succession in many separate areas of the community and hence produce a maze of so-called "regressive" and progressive areas.

Sernander's view.—Sernander (1910:208) has drawn a distinction between progressive and regenerative development:

"The real cause why the *Sphagnum* peat is heaped up in such fashion lies in the fact that the moribund parts lag behind the living *Sphagnum* in growth, and finally form hollows in the latter. These hollows fill gradually with water, while the erosion of the surrounding peat-walls increases their extent. In the water arise new *Sphagneta,* which begin in miniature the progressive development, which I term *regeneration*. This regenerative development of the hollows soon culminates in *Calluna*-heath or is interrupted by a new formation of hollows. The latter develops in the usual way, and in this manner arises one lens-shaped peat-mass above another, characterized above and below by dark streaks, usually of heath-peat."

In discussing the origin of the high moor of Örsmossen (1910:1296) Sernander states that:

"After the progressive development, where regeneration plays a relatively minor rôle, appears a stage in which the moor passes simultaneously into heath-moor over large areas with uniform topography. (In the deeper hollows, the progressive development may proceed further.) In the sequence of the layers, the lower *Sphagnum* peat is followed by a more or less coherent layer of heath peat. With the development of the heath moor begins the formation of hollows, and the accumulation of regenerative peat masses, commonly with great sods of *Andromeda-Sphagnum* peat and *Scheuchzeria-Sphagnum* peat directly above the peat of the heath moor."

Sernander's description of the formation of hollows by the death of the peat and of the consequent production of tiny pools which are invaded by *Sphagnum* furnishes outstanding proof that the retrogressive development of Nilsson and Cajander is actually the death of a plant community or a part of it, and the resulting formation of a bare area for colonization. No serious objection can be brought against the use of the term *regeneration* or *regenerative development,* and it has the advantage of being in harmony with the idea that succession is a reproductive process. It does, however, obscure the fact that the development is nothing but the normal progressive movement typical of succession. It is normally secondary, but differs from the primary progressive development only in being shorter and in occurring in miniature in hundreds of tiny areas.

Moss's view.—Moss (1910:36) makes the following statements in regard to the direction of movement:

"Succession of associations within a formation may be either progressive or retrogressive. In the salt marshes in the south of England for example, a succession of progressive associations of *Zostera,* of *Spartina,* of *Salicornia,* etc., culminates in a comparatively stable association of close turf formed of *Glyceria maritima.* The latter association, however, may be attacked by the waves and ultimately destroyed; and thus retrogressive associations are produced. In the case of established woods, we do not know the progressive associations which culminated in the woodland associations; but we can determine retrogressive stages through scrub to grassland. Similarly, the retrogressive associations which are seen in denuding peat moors are recognizable.

"A plant formation, then, comprises the progressive associations which culminate in one or more stable or chief associations, and the retrogressive associations which result from the decay of the chief associations, so long as these changes occur in the same habitat.

"It sometimes happens, as in the case of the peat moors on the Pennine watershed, that the original habitat is wholly denuded and a new rock or soil surface laid bare. In other cases, as when sand-dunes are built up on the site of a pre-existing salt marsh, a habitat may be overwhelmed by a new one. In such cases the succession passes from one formation to another formation. Again, a new habitat is created when an open sheet of water is choked up with silt and peat.

"Every formation has at least one chief association; it may have more; and they may be regarded as equivalent to one another in their vegetational rank. They are more distinct and more fixed than progressive or retrogressive associations. Open progressive and retrogressive associations, however, fre-

A. Denudation in moorland, the peat-hags capped here and there with bilberry (*Vaccinium myrtillus*); "retrogression" of the cotton-grass moor (*Eriophoretum*).

B. Degeneration of beechwood due to rabbits, Holt Down, Hampshire, England.

quently occur in formations whose chief associations are closed. Unless, however, the progressive and retrogressive associations are included in the same formation as the chief associations, an incomplete or unbalanced picture of the vegetation results."

In the first paragraph the real identity of retrogression with destruction and denudation is clearly indicated by the author in the statements that the stable association of *Glyceria maritima* may be destroyed by the waves, and that retrogressive associations are recognizable in denuding peat-moss. Moreover, he ignores the part light plays in determining habitat limits, and consequently the normal developmental relation of reaction to changes of population. The production of new areas by denudation and by deposition is distinctly pointed out, but the essential correlation of this with succession is not made (plate 19 A).

The views of Moss were adopted by Tansley and several of his associates, Moss, Rankin, and Lewis, in "Types of British Vegetation" (1911):

"The different types of plant community on the same soil, namely, 'scrub' or bushland, and a corresponding grassland, or heathland, have no doubt originated mainly from the clearing of the woodland, and the pasturing of sheep and cattle. This prevents the generation of the woodland, and of most of the shrubs also, if the pasturage is sufficiently heavy and continuous, while it encourages the growth of grasses. Thus the plant formation determined by the particular soil, and once represented by woodland, shows a series of phases of degeneration or retrogression from the original woodland, brought about by the activity of man. The intimate relationship of the various phases is clearly seen in the associated plants. The woodland proper has of course a ground vegetation consisting of characteristic shade plants, but the open places, and the 'drives' and 'rides' of the woods, are occupied by many of the species found among the scrub and in the grassland, while those true woodland plants, which can endure exposure to bright light and the drier air outside the shelter of the trees, often persist among the grasses of the open. In some cases where grassland is not pastured, the shrubs and trees of the formation recolonize the open land, and woodland is regenerated. Besides these degenerative processes, due to human interference, there are others due to 'natural' causes, which are for the most part little understood." (17)

The degeneration of *Quercetum roburis* into subordinate or retrogressive associations of scrub and grassland is described (page 83), and the similar behavior of *Quercetum sessiliflorae* is discussed (page 130). An instructive discussion of reproduction in beechwood (168) lays bare the successional relations of the beech and ash, and at the same time serves to emphasize the fact that so-called degeneration is not a developmental but a destructive process due to man and animals. The last statement is also true of the behavior of heather moors, in connection with their repeated destruction by burning every few years (277) (plate 19 B.)

The degeneration (retrogression) of moorland (280) obviously consists of two processes: "The earlier stages of the degeneration of a cotton-grass moor, in which the wetter *Eriophoretum vaginati* is replaced by the drier *Vaccinietum myrtilli* owing to gradual desiccation of the peat by improved drainage," are merely a normal stage of progressive development in which a hydrophytic sedge is replaced by a more mesophytic shrub. The sequence of life-forms and the reaction upon the water-content both prove that the movement is pro-

gressive and truly developmental, the drying due to erosion merely hastening the normal reaction. This is further proved by the statement that:

"The five upland moor associations and their transitional forms described in the preceding pages form a series, *Sphagnetum, Eriophoretum, Scirpetum, Vaccinietum,* and *Callunetum,* showing a decreasing water content. . . . The desiccation of the peat may be continued till the moor formation is completely destroyed. The first effect upon the vegetation is, as we have seen, the disappearance of the cotton grass and the occupation of the peat surface by the bilberry (*Vaccinium myrtillus*), the crowberry (*Empetrum nigrum*), and the cloudberry (*Rubus chamaemorus*). As the process of denudation continues, this association gradually succumbs to changing conditions until the peat-hags become almost or quite destitute of plants. The peat, being no longer held together, is whirled about and washed away by every rainstorm or by the waters of melting snow.

"In the end, the retrogressive changes result in the complete disappearance of the peat, and a new set of species begins to invade the now peatless surface."

This is a convincing picture of the normal destructive action of erosion in producing new areas for succession, and the apparent retrogression or degeneration of the moor thus resolves itself readily into the usual progressive movement of the dwarf-shrub stage, and the more or less rapid destruction of the latter, as well as the cotton-grass stage, by erosion. Destruction by erosion is also the explanation of the "phase of retrogression" found in the dune succession when the "seaward face of the dunes is eaten away by the waves."

Finally, Moss (1913) has extended the idea of retrogressive associations to include, it would seem, the larger number of communities in the Peak district of England. In discussing the degeneration of woodland (91), the author himself appears in doubt as to the natural occurrence of such a process. He says:

"There can be no doubt that a certain amount of the degeneration of the woodland of this district has been brought about by the indiscriminate felling of trees, the absence of any definite system of replanting, and the grazing of quadrupeds. It is doubtful, however, if these causes are quite sufficient to account for so great a lowering of the upper limit of the forest as 250 feet (76m.) and for so general a phenomenon. . . . It would appear to be true that, in districts which are capable on climatic and edaphic grounds of supporting woodland or true forest, the majority of examples of open scrub are to be regarded as degenerate woods and retrogressive associations. (94) . . . It would appear to be indubitable that woodland is frequently displaced by associations of scrub, grassland, heath, and moor. In all parts of the British Isles there has, within the historical period, been a pronounced diminution of the forest area, a diminution which, in my judgment, is in addition to and apart from any artificial deforestátion or any change of climate. (96) . . . The conversion of woodland into scrub and of scrub into grassland, heath, or moor is seen not only on the Pennines, but in Wales, in the Lake District, and in Scotland. . . . Such successions are not exceptional in this country, but widespread and general; and whilst they are without doubt often due, in part, to artificial causes, it is at least conceivable that this is not always and wholly the case." (96)

In an earlier paper (1907:44, 50), Moss states that ash-copse furnishes "the preliminary stages of a naturally forming ash-wood, or sometimes a

vestige of a former extensive ash-wood," and apparently holds the opinion that "progressive" scrub is more frequent than "retrogressive" scrub. It is difficult to discover the reasons for his change of opinion. The absence of definite evidence of degeneration, and especially of retrogression, due to natural causes, militates strongly against the acceptance of his later view. The question of supposed degeneration is preeminently one in which quantitative methods through a number of years are indispensable. Quadrat and transect must be used to determine the precise changes of population and of dominance. Changes of habitat and the degree and direction of reactions must be determined by intensive methods of instrumentation, while the exact developmental sequence can only be ascertained by the minute comparative study of scar-rings and stump-rings, as well as that of soil-layers and relicts. Even the keenest general observations can not take the place of exact methods, which are alone capable of converting opinion into fact.

Moss considers retrogression of the moor upon pages 166, 188, and 191. The point already made that the *Vaccinietum myrtilli* is always a stage in the normal progressive development is confirmed by the classification of moorland plant associations. (166) The discussion of retrogressive moors (188-189) adds further emphasis to the fact that retrogression is merely destruction due to denudation.

"Whilst the peat of the closed association of *Eriophorum vaginatum* is still increasing in thickness at a comparatively rapid rate, and that of the closed associations of heather and bilberry is also increasing though much more slowly, the peat on the most elevated portions of the moors is gradually being washed away. This process of physical denudation represents a stage through which, it would appear, all peat moors, if left to themselves, must eventually pass. Following Cajander [*cf.* Nilsson, p. 146], the associations thus formed are termed retrogressive ['regressive'] associations.

"In the Peak District, the process of retrogression in the cottongrass moors is apparently initiated by the cutting back of streams at their sources. Every storm results in quantities of peat being carried away, in the stream winning its way further back into the peat, and in the channels becoming wider and deeper. Numerous tributary streams are also formed in the course of time, and eventually the network of peaty channels at the head coalesces with a similar system belonging to the stream which flows down the opposite hillside. The peat moor which was formerly the gathering ground of both rivers is divided up into detached masses of peat, locally known as peat hags and the final disappearance of even these is merely a matter of time.

"It is obvious that this process results in a drying up of the peat of the original cottongrass moor; and it is most interesting to trace a series of degradation changes of the now decaying peat moor. The first change of importance of the vegetation appears to be the dying out of the more hydrophilous species, such as *Eriophorum vaginatum* and *E. angustifolium*, and the increase, on the summits of peaty 'islands' or 'peat-hags,' of plants, such as *Vaccinium myrtillus* and *Empetrum nigrum*, which can tolerate the newer and drier soil conditions. The composition of the upper layers of the peat of these retrogressive moors has, during the course of the present investigation, been carefully examined; and it has been found that the peat consists in its upper layers almost wholly of the remains of *Eriophorum*. The succession of cottongrass moor to the series of retrogressive moors here being described, is established beyond a doubt."

Hole's view.—Hole (1911:13) defines progressive succession as follows:

"A succession which thus proceeds from a xerophilous to a mesophilous and finally a hygrophilous type of vegetation, *i. e.*, from a simple to what must be regarded as a more highly developed type, may be termed a *progressive* succession. On the other hand, the reverse succession from a highly developed to a more simple type may be termed *regressive*. An example of such a succession is seen when mesophilous forest is cleared, or more gradually destroyed by fire and grazing, the resulting erosion on steep slopes converting the area into a rocky hillside only capable of supporting the poorest and most xerophilous types of vegetation. Fire is a very potent factor in causing regressive successions, for it is not only capable of temporarily depriving the soil more or less completely of its covering of vegetation, but it also directly dries the soil and destroys the humus. Fire may in this way be responsible for the existence of xerophilous grassland, or woodland, in localities which once supported mesophilous or possibly hygrophilous, vegetation. Grazing again, by destroying the undergrowth and keeping a forest open, may so reduce the humus content of the soil as to render impossible the reproduction of the mesophilous species constituting the forest and may thus cause a regressive succession. Coppice fellings in the middle of a forest may similarly cause a regressive succession.

"Finally there is a type of succession which we may distinguish as *parallel* succession. Types of both grassland and woodland are found in all kinds of habitats, ranging from the most xerophytic to the most hygrophytic, and it is of great importance to realize that for each type of grassland there is as a rule a corresponding type of woodland capable of thriving under similar conditions of environment, seeing that this has a direct bearing on the afforesting of grasslands. When a type of grassland, such as Munj savannah, is replaced by a parallel type of woodland, *e. g.*, dry miscellaneous forest of *Acacia*, *Dalbergia*, and others, we may therefore regard it as a case of parallel sucession to distinguish it from the progressive and regressive changes considered above. Parallel changes can be effected more easily and rapidly than progressive changes, and with reference to such questions as the afforestation of grasslands and the extension of woodlands, parallel changes are as a rule of more importance."

The author regards wet savannah, reed-swamp, and tropical evergreen forest as hygrophilous formations. Of these, the reed-swamp is usually regarded as hydrophytic, and, in extra-tropical regions at least, it never forms a final stage in succession. While Hole is evidently seeking the climatic climax in his definition of progressive succession, it seems doubtful that wet savannah and reed-swamp can be regarded as such. His view that progression passes through mesophytic stages to hygrophilous or hydrophytic ones is at variance with that of Cowles, in which mesophytic stages form the climax. While Cowles also regards movement from hydrophytic to mesophytic communities as progression, Hole does not consider this sequence at all. This conflict of opinion serves to emphasize the necessity of dealing with development alone, quite irrespective of the water character of the final stage. The author's statement that the progressive succession "proceeds from a simple to what must be regarded as a more highly developed type" is sound. But the types must be arranged upon the basis of life-form or phyad, and not upon habitat-forms determined by water.

Hole's definition makes it clear why it was necessary for him to recognize a parallel succession. From the basic standpoint of development, parallel succession is but the universal progression from lower to higher phyads characteristic of all seres. This is clear from the citation given above, but it is also shown by the following:

"A very clear case where an area of recent alluvium has been first colonized by munj (*Saccharum munja*) in this way, but from which it has later been driven out again by the khair (*Acacia catechii*), has been seen by the writer in an area at the foot of the southern slopes of the Siwaliks near Mohan. In part of the area, munj is still dominant and vigorous, but young plants of khair are just appearing scattered here and there; in other portions the khair are more numerous, larger and older, and many of the munj clumps between them can be seen dead and dying, while elsewhere a dense pure polewood of khair has become established under the shade of which can still be seen the decayed remains of the munj clumps which had first colonized the spot."

Regression is defined as the "reverse succession from a highly developed to a more simple type." The illustrations given have been quoted above. It is again evident in these examples that the process is merely one of destruction by lumbering, fire, grazing, or erosion, with subsequent colonization by lower types. There is no succession, no development from forest to grassland, but a replacement of forest by grassland as a consequence of more or less complete destruction of the trees. As in all cases of supposed regression, the actual facts, in partially denuded areas especially, can be obtained only by quadrat and instrumental methods lasting through several years.

Conversion of forest.—The foregoing accounts seem to make it clear that nearly all cases of so-called retrogression or regression are not processes of development at all. They are really examples of the initiation of normal progressive development in consequence of destruction or denudation. Hence it is incorrect to speak of retrogressive succession or development, as well as of retrogressive formations or associations. The latter are merely those stages in which the production of a bare area occurs, with the concomitant origin of a new sere. Furthermore, the diverging views upon the subject indicate that the analysis has been superficial and extensive rather than intensive and developmental.

There remain to be considered those cases in which a change from a higher climax community to a lower subclimax community actually occurs. Such are the actual and supposed cases of the conversion of forest into scrub, heath, grassland, or swamp. The supposed examples of this change are numerous, but the process of conversion has been seen and studied in very few instances. This does not mean that the process may not be as universal as its advocates assume, but it does indicate that the final acceptance of this view must await intensive quantitative study of typical cases in each association. In this connection there are three distinct questions to be considered: (1) is it actually proven that the conversion of forest into heath or grassland does occur; (2) can this change be produced by natural as well as artificial agencies; (3) is it an actual successional development in a backward direction.

Superficial evidence of the change of forest into grassland or heath is abundant in all countries where lumbering, grazing, and cultivation have been pursued for centuries. The rise of ecology is so recent, however, and the number

of intensive quantitative studies for a period of years so few that there is hardly a case in which conclusive proof is available. The well-nigh universal opinion of European workers in this matter merely constitutes an excellent working hypothesis, which can be accepted only after the most rigorous tests by exact ecology. The literature upon this subject is vast, but while much of it is suggestive, little is convincing. The dearth of conclusive evidence may best be indicated by the following statements from recent investigations. Graebner (1901:97) says:

"In spite of the numerous moors with roots and upright stems that I have seen, for a long time I was unable to discover the swamping of a forest in the actual beginning of development. Finally, however, I had the opportunity of seeing two such moors in process of formation. One of these was found near Salm in western Prussia, the other at Kolbermoor in upper Bavaria."

Status of forest in Britain.—The difficulties of determining the actual changes of woodland in the past may be gained from the statement of Moss, Rankin, and Tansley (1910:114):

"In a country like England, much of which has been cultivated and thickly populated for centuries, it may be asked, do there remain any natural woodlands at all? Have not existing woods been so altered by planting and in other ways that they no longer represent the native plant communities, but are rather to be considered as mere congeries of indigenous and introduced species?

"It is undoubtedly true that there is little 'Urwald' or true virgin forest remaining in the country, though some of the woods, especially near the upper limit of woodland in the more mountainous regions, might make good their claim to this title. On the other hand, there are, of course, many plantations pure and simple which have been made on moorland, heath, grassland, or arable land, and which may of course consist of native or of exotic trees or of a mixture of the two. But between these two extremes, according to the conclusions of all the members of the British Vegetation Committee who have given any special attention to this subject, come the great majority of the British woods; which are neither virgin forest, nor plantations *de novo,* but are the lineal descendants, so to speak, of primitive woods. Such semi-natural woods, though often more or less planted, retain the essential features of natural woods as opposed to plantations, and without any reasonable doubt are characterized by many of the species which inhabited them in their original or virgin condition."

Moss (1913:111) concludes that:

"Whilst opinions may differ as to whether or not the grassland just described is wholly or only in part due to man's interference, it appears to be generally accepted that such tracts were formerly clothed with forest; and Warming (1909:326) even goes so far as to say that 'were the human race to die out,' the grasslands of the lowlands of northern Europe 'would once more be seized by forest, just as their soil was originally stolen from forest.' As regards the Nardus grassland of the hill slopes of this district, it seems incontestable that it is an association which has, on the whole, resulted from the degeneration of oak and birch woods. The fundamental conditions of the habitat have been but slightly altered in the process; and, therefore, the oak and birch woods, the Nardus grassland, and the various transitional stages of scrub are placed in one and the same plant formation."

In America, the questions of the origin of the prairies, their derivation from forest, and their present tendency to become forest, have produced a copious literature, but the latter contains little or no conclusive evidence for one view or the other.

Artificial conversion.—In spite of the almost total lack of direct proof, there is so much observational evidence of the artificial conversion of forest into scrub, heath, moor, or grassland as to create a strong presumption in favor of this view, and to furnish the most promising working hypotheses for intensive investigation. In the innumerable cases of the destruction of forest by cutting, grazing, fire, or cultivation, and the establishment of a subclimax, the feeling often amounts to positive conviction, which needs only experimental proof to be final. Indeed, many ecologists would doubtless regard the latter as altogether superfluous in most cases. In fact, one may well admit that all the evidence in our possession confirms the frequent change of forest to scrub or grassland where artificial agencies are at work. There is grave doubt when we come to consider the effect of natural causes in producing such changes. At present there is no incontestable proof of the conversion of forests by natural causes, except of course where effective changes in climate or physiography intervene. Graebner (1901:69, 97) has summarized the results of his own studies, as well as those of other investigators, and has furnished strong if not convincing evidence that forest may be replaced by heath or moor. It is significant, however, that in the various processes described by him, with one possible exception, the cutting of trees or an increase of surface water is required to initiate the changes which destroy the trees, and permit the entrance of *Calluna* or *Sphagnum*. In short, conversion is typically the consequence of destruction and subsequent progressive development, often obscured by the fragmentary nature of the areas concerned.

Graebner's studies (1901): Conversion of forest to heath.—Graebner's description of the process is so detailed and so convincing that a full account of it is given here.

"Let us picture to ourselves the conversion to heath of a particular forest, such as may have obtained on the Lüneberg Heath with the disappearance of the great forests. The calcareous pernutrient soil bears beech wood. The latter is completely removed as a consequence of the great demand for wood. While the ground remains bare and the forest slowly renews itself, the leaching-out of the nutrients in the soil proceeds more intensively, since the water formerly caught by leaves and mosses, and then evaporated, now soaks into the soil. Finally the forest again becomes closed, and then mature, and is again cut down. This may recur several times, during which the leaching-out of the upper layers in particular progresses steadily. With the decrease of nutrients in the upper layers, the growth of the herbs is made more and more difficult, until finally these die out, since their roots are unable to reach into the deeper unleached layers of soil. As a consequence, all herbs which demand relatively large amounts of nutrients are excluded. The competition of plants with low requirements and slow growth disappears, and leaves the field to heath plants.

"At first the heath plants colonize but sparsely beneath the trees. In such a forest, one sees a few heath plants here and there, especially *Calluna,* which have however a suppressed look because of the deep shade still found in most places. The growth of tree seedlings in the poor sandy soil becomes greatly

handicapped. Seeds of the beech germinate normally, but in the first few years the seedlings show only a weak growth, especially of the aerial parts, as a consequence of the poor soil. Ultimately, the growing roots reach the lower richer soil layers, and the young saplings then begin to stretch upwards. They develop dense thickets in the gaps due to fallen trees, and thus hinder the further development of heath plants. Such forests have mostly a very poor flora, since forest plants lack for nutrients, and heath plants are suppressed by the dense shade. In such places, a complete conversion to heath could occur not at all or only after a long period, since the layer of leached soil must attain such a thickness that the seedlings disappear before their roots reach the deeper nutrient layer. In this event, it is more probable that the beech will be replaced by a tree with lower requirements, such as the pine, before this finally yields to the heath.

"The formation of 'ortstein' hinders the reproduction of the forest, as soon as the leached layer becomes so thick that frost can not penetrate to its lower limit. At this level, the precipitation of dissolved humus compounds, leached out of the soil above, cements the sand into a humus sandstone. In the heath regions, the latter is laid down for miles as a pure uninterrupted layer at a depth of one foot as a rule. As soon as the 'ortstein' has attained a certain thickness and density, it can not be pierced by plant roots. The latter can penetrate only in small gaps which maintain themselves here and there in the layer. The upper leached layer is thus almost completely separated from the lower nutrient layer. The variations in water content are marked and can no longer be affected by capillarity. As soon as the 'ortstein' begins to develop in the forest, the latter takes on a different look. The roots of beech seedlings and of young plants of the undergrowth can not penetrate the 'ortstein' and reach the lower soil layer. They languish for a time, and then perish as a consequence of lack of nutrients and water, or of the winter killing of the unripened wood. Undergrowth and reproduction begin to disappear. The gaps produced by the fall of old mature trees are not filled with new growth, and thus afford favorable conditions for heath vegetation. The forest becomes more and more open through the death of old trees, the heath develops correspondingly, and soon becomes dominant. After a few decades only isolated trees remain upon the bare field. Elsewhere all is heath.

"Such are the general features of the process by which the vast stretches of heath have arisen from forest. To-day we have all stages of the development of deciduous wood of beech and oak to typical heath, especially in the eastern transition regions. Conversion to heath is naturally hastened by the clearing and utilization of the forest, though it must occur even without this, through the operation of climatic factors upon sandy soil.

"The conversion of pine forest into heath is quite similar to that of beech forest, though the lower requirements of the pine enable its seedlings to thrive better in the leached soil. The leaching-out process also proceeds more rapidly owing to the lower nutrient content, but the development of 'ortstein' is less marked. This is due to the fact that the looser canopy of the pine forest, as well as the sparser undergrowth, permits the sun and the wind to hasten decomposition, in relation to humus production. On the protected floor of the beech forest, on the contrary, the formation of humus is more marked than decomposition, and there is in consequence a larger supply of humus compounds for precipitation as the cement of 'ortstein.'

"A further method of heath formation is considered by Grebe (1896). In this, the decomposition of the fallen needles or leaves takes place so slowly in dense shady woods, especially of fir and in moist climates, that by far the

bulk of the material is converted into humus, which gradually compacts itself into a firm layer. Heath formation on such a soil is interesting for the reason that it may occur without the leaching of the upper layer, and indeed may be found on heavy loam or clay. Grebe describes the action of the raw humus upon vegetation as follows: '(1) The raw humus cuts off the lower soil almost completely from its air supply. (2) It hinders the circulation of water in the soil. It prevents the evaporation of superfluous moisture in winter and spring, and in summer it hinders the penetration of light rains and of dew. (3) It is probable that the soil beneath the layer of heath-felt passes out of the stage of oxidation into that of stagnation and reduction. (4) The upper soil layer is relatively poor in dissolved mineral salts, the middle and lower relatively rich. (5) While the raw humus of the heath is as rich as the humus of the beech woods and pine woods, it is so firmly combined as a consequence of its peaty nature that it can not be used by the trees.'

"Grebe has been correct in his assumption that the aeration of the soil is almost completely prevented by the raw humus. According to my opinion, this factor suffices almost entirely alone to make the proper growth of trees impossible and to call forth sickness, stunting, or death according to the intensity of its action."

Conversion of forest into moor.—"It is generally recognized that the heath moor differs from the meadow moor in that it is not level but convex. It grows upward not only in the middle, but also, even though slowly, at the margin. Now if such a moor arises in a shallow depression, it slowly pushes its edges up the slopes. Thus it finally reaches a gap in the surrounding hills, and it then extends a tongue through the gap into further levels. Thus it comes about that a lively movement of water is noticed, when the tongue of the moor lies upon sloping ground. Since the tongue lies lower than the surface of the moor and the *Sphagnum* holds the water so firmly that the surplus can soak into the soil but slowly, the tongue is constantly dripping with water, and in most cases a quantity of water flows away from it, as at Kolbermoor. If the soil of the slope and adjacent lower areas is not especially pernutrient at its surface, the formation of heath moor proceeds rapidly. The cushions of *Sphagnum* spread more and more widely till they reach the bottom of the low area always fed with water from above. The bottom once reached, the constant flow furnishes abundant water for further development, unless, as is frequently the case, a colony of *Sphagnum* has already occupied the bottom as a consequence of the accumulating water, in which event the two masses unite. Whenever the hollow or the slope and gap are covered with forest, the soil is converted into swamp by the *Sphagnum* and the air is driven out as a result. The physiological effect upon the growth of trees is the same as in the formation of raw humus upon the forest floor. It is a peculiarly desolate picture that is formed by the countless dead standing trunks in a young moor. One trunk after another falls, and soon they are all buried in the moor, and nothing visible remains to remind one of the former forest.

"In order to exhibit the entire process of the swamping of a forest, I have purposely chosen cases in which the moor must pass over a small elevation, since the important events in the water movement are much clearer than in the common instances. For the most part, the formation of heath moor upon meadow moor, or also in lowland forest, takes place completely on the level, and in the following manner. The lowlands have become filled with meadow moors [swamps], as a result of the forlanding of ponds and lakes, and the consequent development of swamps. The ground level of the swamp slowly grows upward because of the annual increment of plant remains, but only to

the point where plants are still able to obtain the necessary water supply. Wherever the swamp is built above the level of the ground water, trees, especially alders and oaks, enter and form forests. Often, however, the swamps remain treeless. The swamp peat has the peculiarity that is conducts water very poorly, in contrast to heath moor peat, which has a marked conductive power. As a result, the swamp plants disappear as soon as their roots are no longer able to penetrate into the subsoil, and at the outset the flat-rooted plants disappear. There remains a community of tall perennials, mostly grasses.

"This is the point at which the change to heath moor begins. *Sphagnum* colonizes the lower moister places, and in similar fashion as upon the moist sandy soils, the cushions run together and first fill the hollows and ditches in the swamp. As soon as the *Sphagnum* has reached a certain extent, and has filled the bottom of a ditch or hollow, other conditions of moisture begin to appear. While previously a single dry sunny day sufficed to dry out and heat up the black surface of the moor, the *Sphagnum* cushions now hold the water with great tenacity. Even after a long dry period, the moss turf is still moderately moist within, while elsewhere it is dried out. In early stages, the *Sphagnum* occurs only in ditches and hollows, which soon become completely filled. When the moss layer has reached a certain thickness, it forms a great reservoir of water, and the upward growth of the moss constantly increases. It then spreads laterally over the level surface of the swamp, always carrying larger quantities of water, which is unable to sink away because of the marked imperviousness of the swamp peat which underlies the heath peat. After a time, the various *Sphagnum* masses grow together and close over the swamp.

"The primary requisite for such a moor, in so far as an actual inflow of water is concerned, is that the annual precipitation should be greater than the loss of water by evaporation and percolation. Here must be noted the fact that the marked affinity of *Sphagnum* and heath peat for water, as well as the very impervious nature of peat when it is saturated, produces very different water relations than those which prevail in the swamp. The dependence of such moors upon the rainfall of a region also explains the great frequency of heath moors in the great heath regions, and their infrequence or absence in dry climates (98-100).

"In cases where a forest has developed upon a meadow moor before the beginning of a moss moor, the development of a heath moor takes place more rapidly. This is obviously due to the protection which the trees afford the *Sphagnum* against sudden drouth. In such forests one almost never finds small scattered cushions, but nearly always great masses or connected mats. In an open swamp in which heath moor is beginning its development, one finds on the contrary that the small dense moss cushions, located in small depressions under the scanty shade of grass tufts, have their stems much compacted and often show a red color. This indicates that the mosses live there only on sufferance, and that they scarcely secure enough water to last through a dry period.

"The second method of origin of heath moor upon bare soil is that found in some meadow moors. One very often finds in moors of great depth that there is at bottom a more or less thick layer of black swamp peat, which passes through a definite zone, often with tree trunks, into the heath peat above. Not rarely, especially in northwestern Germany, the heath peat shows an upper and lower layer. The development of heath moor in swamp in such cases must have been due to a change of water relations, as a consequence of which the swamp was flooded with enutrient water. Such instances

must, however, occur but rarely. In the majority of cases, heath moor arises in a swamp very much as it does in forest. It is best in consequence not to separate the consideration of the two, especially since the sections of moors show that a layer of tree roots is very often found at the edge of the swamp or heath moor layers. Such a moor was forested before it became covered with heath moor." (96)

Causes of conversion.—Graebner has described six processes by which forest or swamp is converted into heath or heath-moor. In the first, forest is changed into heath as a result of the removal of the trees in whole or in part, with consequent leaching of the upper layer and the formation of "ortstein." The need for destroying the reaction control of the trees, *i. e.*, their shade, is shown by his statement that *Calluna* has a suppressed appearance because of the deep shade still found in many places. The artificial destruction of the forest seems requisite. Graebner says that "the conversion to heath is naturally hastened by the cutting and utilization of forest, though it must occur even without this, through the operation of climatic factors upon soil." Our present knowledge seems quite inadequate to confirm this statement. On theoretical grounds, such conversion would seem quite impossible without the contributing action of climatic variation, since a climate constantly like that under which conversion occurs would have prevented the development of the original forest. The work of Douglass (1909, 1914), Humphreys (1913), and Huntington (1914), seems to indicate clearly that so-called changes of climate are but the persistence for a time of variations such as occur from year to year. It seems probable that the conversion of forest into heath as a result of the formation of raw humus is a consequence of such climatic variations, and that it is further aided by the influence of man and domesticated animals. Graebner himself nowhere considers this matter of climatic oscillations, since he is concerned primarily with the detailed changes in the soil. It is, however, of the most vital importance in determining the real nature of secondary development, since regression can be said to occur only when the reactions of the undisturbed vegetation produce an actual backward sequence of communities.

Of the four ways by which heath moor may arise from an existing swamp or forest, one, the flooding of a swamp by enutrient water, is obviously a matter of destruction and denudation. A careful analysis of the other cases likewise shows that the process is here one of flooding and destruction. The essential fact that the change is due to flooding is obscured by the intimate interrelation between *Sphagnum* and water, and by the appearance of *Sphagnum* in many separate spots. Ecologically, the water-soaked moss is the equivalent of the direct flooding of an area by so much water, except that the *Sphagnum* water has a much more marked effect, since most of it can not drain off, and since the amount constantly increases. The *Sphagnum* is really a pioneer in a new if minute water area, and differs only in degree from the thalli of algal pioneers, such as *Nostoc,* which also absorb and retain water tenaciously. Graebner's statements also support this view, for he says:

"This is the point at which the change to heath moor begins. *Sphagnum* colonizes the lower moister places and, in similar fashion as upon the moist sandy soils, the cushions run together and first fill the hollows and ditches in the swamp. The *Sphagnum* cushions now hold the water with great tenacity.

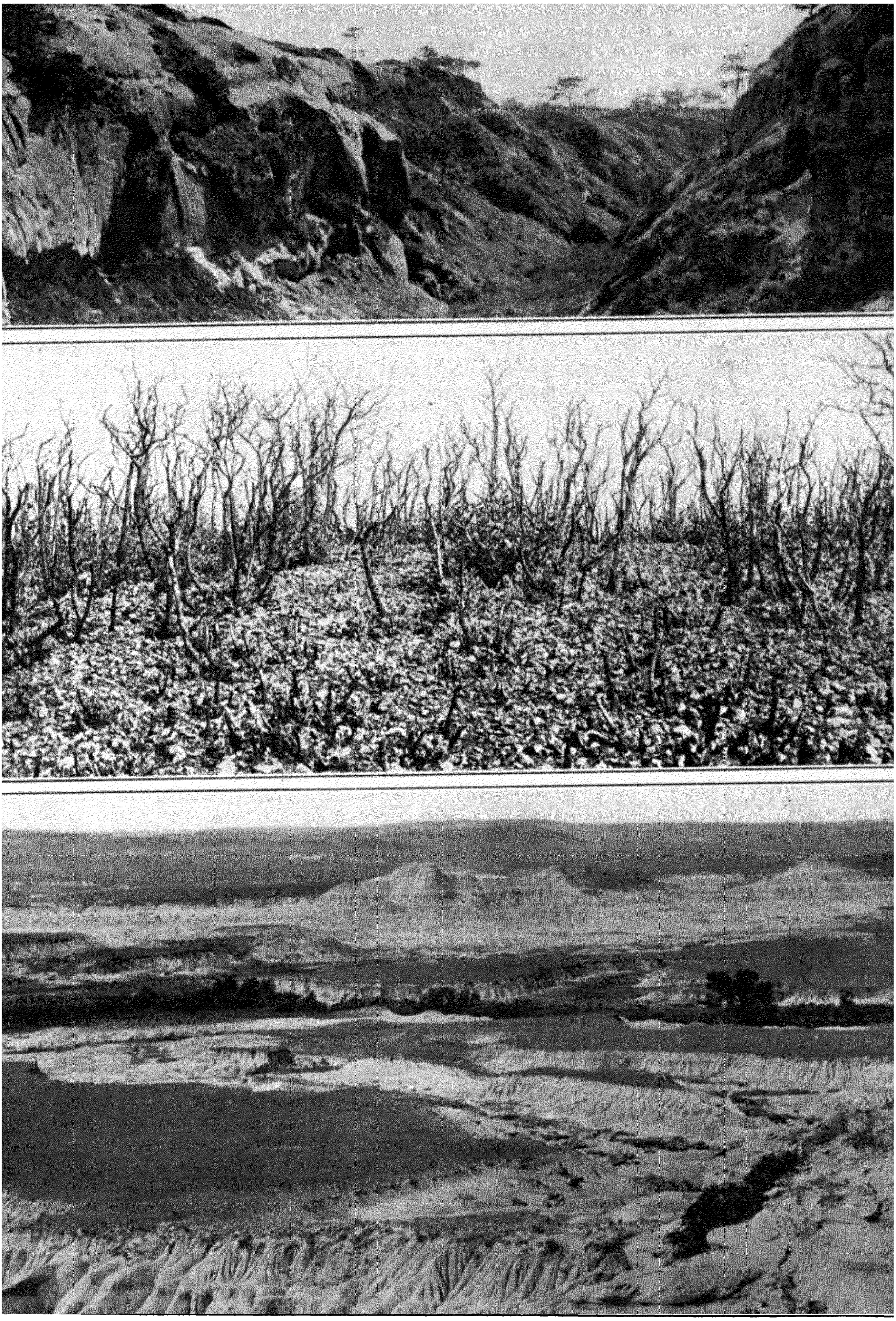
When the moss layer has reached a certain thickness, it forms a great reservoir of water. It then spreads laterally over the level surface of the swamp, always carrying larger quantities of water.

"Since the tongue (of moss-turf) lies lower than the surface of the moor and the *Sphagnum* holds the water so firmly that the surplus can soak into the soil but slowly, the tongue is constantly dripping with water, and in most cases a quantity of water flows away from it. The bottom once reached, the constant flow furnishes abundant water for further development, unless, as is frequently the case, a colony of *Sphagnum* has already occupied the bottom, as a consequence of the accumulating water. The soil is converted into swamp by the *Sphagnum* and the air is driven out as a result."

These are the precise consequences of ordinary flooding by water, and likewise lead to destruction of the grassland or forest.

To sum up, while there is abundant evidence that forest is being changed into scrub, heath, or grassland as a result of the action of artificial causes, there is no convincing proof that such conversion can occur under existing natural conditions. In all cases cited, disturbance by man is either a certain or probable factor, or the destruction has been a consequence of topographic or climatic changes. In no case is there clear proof, as a result of continued quantitative investigation, that a forest produces changes inimical to its existence and favorable to a lower type of vegetation.

Possibility of backward development.—In all cases of the change of forest to scrub or grassland, even if they be admitted to result from artificial disturbance in some degree, it would seem at first thought that the process is actually a backward development, *i. e.*, retrogression. In all the instances cited above, however, as well as in all of those so far encountered, the only development is that of a new community on ground left partially or completely bare by the forest. There is no difficulty at all in recognizing this when the ground is entirely denuded by a fire, and but little when the trees are completely destroyed by clean cutting. Similarly, when areas of some extent are cleared in the forest, it is sufficiently obvious that the communities which appear in the clearing are the result of the destruction of the former dominants, and of consequent invasion into a sunny though localized habitat. When, however, such areas are no larger than the space made by the fall or removal of a single tree, the situation is more complex. A comparison of a number of such small areas, alternating with each other as well as with clearings of various size, would give the impression of an actual retrogression. This would be due to the amount and kind of invasion in denuded areas of widely differing extent, and the consequent persistence or adaptation of the original undergrowth in varying degrees. Indeed, a general comparison of such areas can not be expected to yield the real facts. It is only by the exact study of each cleared area, large or small, that the true nature of the process stands revealed. Such an investigation will invariably show that, no matter how small an area may be, it has a progressive development all its own, but in every respect in essential harmony with the development in a large clearing of the same forest, or in an extensive denuded area of the same type. In every case it is found that there is no backward development, but merely a fictitious appearance of it due to destruction of the dominants in large or small degree, and the immediate invasion of species best adapted to the conditions of the new area. The care-



A. Destruction of woodland of *Pinus torreyana* by fire and erosion, and replacement by chaparral, Del Mar, California.

B. Root-sprouting from the base of burned chaparral dominants, *Quercus*, *Arctostaphylus*, etc., Mount Tamalpais, California.

C. Destruction of mixed prairie and invasion by woodland and scrub, bad lands, Crawford, Nebraska.

ful scrutiny and investigation of thousands of cases of local or minute denudation in various associations permit of no other conclusion (plate 20).

An actual retrogressive development, a regressive succession, would necessarily move backward through the same communities, represented by the same phyads and reactions, as those through which the sere progressed. No one has yet furnished the slightest evidence of such a development, and according to the views set forth here, such a movement is absolutely impossible. It can no more take place than an adult plant can be devolved again into a seedling or a seed. The adult plant may be destroyed, and the seedling may take its place. In like manner, a climax or subclimax community may be destroyed, and an earlier associes develop in its stead. But a backward development is as impossible in the one case as in the other. Destruction and reproduction are the only possible processes. Even if one were to attempt to remove all the individuals of each community in the reverse order of sequence, a true retrogression comparable with the normal progression would still be impossible, without at the same time destroying the reactions *pari passu* and establishing the dominants of the next earlier associes.

That the development after lumbering is the normal progression due to partial denudation is shown by the observation of Adamović (1899:144) in the Balkans. He summarizes the secondary succession as follows: The first stage occurs a few months after cutting. It is characterized by the disappearance of shade plants, *Oxalis, Actaea, Daphne, Dentaria,* etc., and the increase of the species found at the margin of the wood, such as *Gentiana, Salvia, Knautia, Digitalis, Senecio,* etc. The second stage is marked after a few years by the development of a scrub of *Corylus, Crataegus, Lonicera,* etc., with an undergrowth of *Poa nemoralis, Rhinanthus, Pyrethrum,* etc. The third stage appears after 8 to 10 years, and is characterized by a young growth of *Fagus, Betula, Acer,* and *Sorbus,* with a height of 5 to 6 feet.

Degeneration.—It follows from the above that communities do not degenerate. They can only be destroyed with greater or less rapidity over larger or smaller areas. As indicated above, there can be no thought of degeneration when a forest is completely removed by fire, flood, or ax. This is too obviously the normal process of denudation and secondary development. But when the destruction is piecemeal, or when it acts through many years, the superficial appearance of the community with its areas of normal structure side by side with bits of earlier stages and actual bare spots seems to warrant the conclusion that the community is degenerating. Such a condition is strikingly shown in the moors of the Pennines. The independent study of each area shows, however, that this is only a complex of moor communities in varying stages of progressive development, alternating with areas exhibiting denudation in different degrees. All so-called degenerating associations are to be explained in the same way (plate 19A).

Regeneration.—While the term "degeneration" is both incorrect and misleading, no such objection can be brought against "regeneration" or "rejuvenation." This follows quite naturally from the fact that succession is always progressive, but never retrogressive. A climax formation reproduces itself in whole or in part, depending upon the degree of denudation. When the latter results in the production of a secondary area, the reproduction is essentially that which occurs in the case of a plant regenerated from a leaf, and the

term "regeneration" might be applied to all secondary succession. Rejuvenation is essentially synonymous, though it would seem to include primary successions rather more readily. The only objection to be urged against them is that their use tends to suggest that some process other than normal succession is concerned. Used as synonyms of succession, they are unobjectionable, though as a consequence they are also of little value.

Correlation of progressive developments.—While all successional development is progressive, the concrete seres of every climax formation may bear a direct relation to the whole course of development. This is fundamentally true of the seres which arise in primary and secondary bare areas and hence are distinguished as primary and secondary seres. The one recapitulates the entire succession, the other repeats only more or less of its later sequence. Seres, moreover, show an essential difference with respect to the direction of reaction, depending upon the nature of the extreme conditions in which they arise. Primary seres may arise on rock or in water, or they may develop on new soil, such as that of dunes or bad lands. While secondary areas do not depart so widely from the climatic mean, they may also be xerophytic or hydrophytic. Though often mesophytic, they are always drier or wetter than the climax area.

The basic developmental relation of every sere is indicated by the terms *prisere* and *subsere*. The one is a concrete example of primary succession, the other of secondary succession. Since they mark a fundamental distinction in the development of a climax formation, their further treatment is deferred to the chapter upon classification.

As water-content is the controlling factor in all succession, either directly or indirectly, it furnishes the best basis for indicating the direction of movement. This arises from the fact that it represents the primary interaction of habitat and community in the course of development. In the origin of every sere, the amount of water is the critical factor, and the rate and direction of development will be recorded more or less clearly in its increase or decrease. There are in consequence three possible bases for distinguishing direction in terms of water-content. These are (1) the actual direction of movement itself, (2) the initial condition, (3) the final condition. It is of interest to note that all of these have been used. Clements (1904:124; 1905:257) made use of the actual successional change in water-content, as well as the final term:

"The direction of the movement of a succession is the immediate result of its reaction. From the fundamental nature of vegetation, it must be expressed in terms of water-content. The reaction is often so great that the habitat undergoes a profound change in the course of succession, changing from hydrophytic to mesophytic or xerophytic, or the reverse. This is characteristic of newly formed or exposed soils. Such successions are *xerotropic, mesotropic*, or *hydrotropic*, according to the ultimate condition of the habitat. When the reaction is less marked, the type of habitat does not change materially, and the successions are *xerostatic, mesostatic*, or *hydrostatic*, depending upon the water-content. Such conditions obtain for the most part only in denuded habitats."

Cooper (1912:198) has made the initial conditions the basis of classification:

"The plant successions leading up to the establishment of the climax forest are conveniently classified in two groups: the xerarch successions, having their origin in xerophytic habitats; and the hydrarch successions, originating in hydrophytic habitats."

Cowles (1901) and Hole (1911), as already mentioned, have used the final condition as a basis for distinction. While both use the terms progressive and retrogressive or regressive, Cowles regards all development toward a mesophytic condition as progressive, while Hole employs this term for movement toward a hygrophilous or hydrophytic climax. The disadvantages of the use of the terms progressive and retrogressive have already been discussed.

The emphasis here laid upon the climax formation as an organic unit with a characteristic development would seem to make terms based upon the course of the reaction and the final condition unnecessary. In all cases the progressive development leads to the highest life-form possible, and the tendency of the reaction upon water-content is usually toward a mesophytic mean. Exceptions occur only in dry regions or in moist tropical ones. Hence the nature of the climax formation indicates the direction of movement, and the terms mesotropic, xerotropic, mesostatic, etc., hardly seem necessary at present. To one who does not know the general conditions of a climax formation, they are useful, but there is little need for them until more hydrotropic and xerotropic seres are known. This does not seem true of the terms hydrarch and xerarch since they indicate the extreme condition in which the seres originate, though they also indicate by inference the general course of development. Since it is the kind of initial bare area which gives character to all the earlier stages of a sere, hydrarch and xerarch are now of much value in introducing a basic distinction into both primary and secondary succession. They suggest the normal movement toward the mesophytic mean, but are hardly applicable to seres which are xerotropic or hydrotropic. As a consequence, it may prove desirable to employ the latter terms for the sake of completeness, even in the present state of our knowledge.

Convergence.—It is obvious that all the seres of a climax formation converge to the final community. No matter how widely different they may be in the pioneer stages, their development is marked by a steady approach to the highest type of phyad possible in the climatic habitat and to a corresponding water-content. The pioneer lichens of a rocky ledge and the pioneer algæ of a pool both initiate seres, which are characterized by increasingly higher phyads and more and more medium water-contents, until both terminate in the climatic climax of both vegetation and water, as, for example, in the grassland of the Great Plains.

This fundamental convergence to a climax is developmental, and not individual or local. Each sere in itself is a unit development which moves in the inevitable direction from bare area to climax. Convergence is visible only in a survey of the succession in the climax association as a whole. The actual situation suggests an imaginary developmental cone formed by lines converging from a broad base of various primary and secondary areas through grassland and scrub to the final climax forest. Thus, while the development in every bare area, *e. g.*, rock-ledge, pond, burn, fallow field, etc., is a unit comprising the whole range from the initial extreme to the climax, the seres taken collectively are identical in one or more of the final stages. Convergence may be upon practically any stage in the succession, but it is usually upon a subclimax stage of grassland or scrub in the case of forest, for example. In addition there is often an earlier convergence of primary seres, especially upon some medial stage.

Cooper (1912:198) has used the term "subsuccession" for the seres which begin on rock-surfaces, in crevices and in rock-pools, and terminate in the formation of a heath-mat. Thus, he distinguishes a rock-surface subsuccession, a crevice subsuccession, and a rock-pool subsuccession of the rock-shore succession. However, he does not apply the term to seres which converge later in the development. The phenomenon is the same whether it appears early or late in succession. It is here proposed to apply the term *adsere* (*ad-*, *to*, implying convergence) to that portion of a sere which precedes its convergence into another at any time before the climax stage. While it is possible to distinguish adseres with respect to convergence in the initial, medial, or subclimax stages, at present it does not seem wise to do so. Likewise, a developmental line formed by the convergence of two or more adseres may itself converge and become an adsere (fig. 5). The use of *subsucession* in this connection seems undesirable because of the fundamental distinction already drawn between succession and sere.

Normal movement.—It is probable that the large majority of all the seres of a climax association pass through their development in the normal manner. All the stages are represented; they follow each other in the usual sequence and progress at about the same rate. But the normal course of development may be disturbed or changed in various ways. Frequently the modification is merely one of rate, and succession takes place in the usual way, but at a faster or slower pace. Distinctions upon the rate of movement can hardly be made at present, as our exact knowledge of succession is still small. There are many seres, however, in which it has been shown that artificial or topographic changes have hastened or retarded the normal course. This disturbance may be so great that the sere is held for a long time in some associes, which in consequence takes on the appearance of a climax. Or, as a result of the absence of the usual climax species, the subfinal stage may become the actual climax.

Apart from such modifications as these in which the sequence is not affected, there are those in which stages are dropped out or interpolated, or in which there is a deflection of the course of movement. The failure of a particular stage to develop is a frequent occurrence in seres with many stages, particularly when the reaction of each is not especially marked. In such cases, the sequence is determined largely by migration, and the relative abundance and nearness of the dominants of two or three associes is decisive. On the other hand, the interpolation of an unrelated stage occurs but rarely, since it can take place only when a new dominant enters the region, as in the case of weeds. A complete change in the course of development apparently can result only from a change of climate. Such changes necessarily affect the climax vegetation, and hence are considered in later chapters.

These various modifications have previously been recognized and distinguished by terms (Clements, 1904:107, 122; 1905:240, 254). *Normal* succession begins with nudation, and passes through the regular sequence to the climax association. *Anomalous* succession occurs when the sequence is destroyed by addition or subtraction, or when the succession is deflected. *Imperfect* succession results when one or more of the ordinary stages is omitted anywhere in the course and a later stage appears before its turn. It will occur at any time when a seral area is so surrounded by dense vegetation that

the communities which furnish the next invaders are unable to do so, or when the abundance and mobility of certain species enable them to take possession before their proper turn, and to the exclusion of the regular stage. When a stage foreign to the succession is inserted, replacing a normal consocies or slipping in between two such, the development may be called *interpolated* succession.

Divergence.—Graphic representations of the development to a climax often show divergence as well as convergence. This is frequently due to the ability of a particular consocies to develop in one seral area but not in another. The corresponding diagram often shows a divergence in such cases when none actually occurs. Usually, however, apparent divergence arises from connecting the development of secondary seres with preceding primary ones, or from the presence of two or more nearly equivalent communities, such as *Scirpus caespitosus* and *Eriophorum,* or the alternation of consocies, such as *Typha, Scirpus,* and *Phragmites,* which may occur separately or variously grouped. Within the same climax formation actual divergence is rare if not impossible. It can occur for a time when a foreign dominant is interpolated and it would take place if climatic changes were to affect one part of a great climax area and not another. On the other hand, while the initial stages on rock, in water, and on dune-sand are identical or similar throughout the northern hemisphere, the final climaxes differ widely. This is a natural consequence of the fact that relatively few species can grow in extreme conditions, and that such species are usually able to migrate widely. As a consequence, a few communities form the pioneer and initial stages of the development of a large number of climax associations. The result is that the corresponding seres diverge just as soon as the initial extremes become modified to the point where the effect of the various climates begins to be felt. Such divergence, however, is a feature only in the composite picture of vegetational development in North America and Eurasia. In the case of each climax formation it is absent.

IX. CLASSIFICATION OF SERES.

Historical.—While the division of successions into progressive and regressive by Nilsson (1899) may be regarded as an early attempt at classification, the first system of classification for successions was proposed by Clements (1904:107, 138; 1905:241). Cowles (1901:86) had already advanced his physiographic grouping of the plant societies in the region of Chicago. While this necessarily threw successions into topographic groups, his whole intent was to classify plant societies or associations upon a genetic and dynamic basis (*l. c.*, 178), and hence he did not consider the classification of successions. Later (1911:161), he discusses the causes of vegetative cycles, and proposes a classification upon this basis. These two systems are the only ones yet suggested, and as they have much in common it is desirable to consider them in detail before taking up the system proposed here.

Clements's system.—This was based primarily upon development, with especial reference to reaction, and secondarily upon initial causes, in which topographic causes were recognized as paramount. The division into normal and anomalous successions, and the subdivision of normal successions into primary and secondary were both based upon development. The subdivisions of primary successions were all grounded upon topographic processes, and those of secondary successions upon topographic and biotic agencies, while anomalous successions were primarily due to climatic changes. The essential features of the classification are indicated by the following outline:

I. Normal successions.
  1. Primary successions.
    (1) By elevation.
    (2) By volcanic action.
    (3) In residuary soils.
    (4) In colluvial soils.
    (5) In alluvial soils.
    (6) In aeolian soils.
    (7) In glacial soils.
  2. Secondary successions.
    (1) In eroded soils.
    (2) In flooded soils.
    (3) By subsidence.

I. Normal successions—*Continued.*
  2. Secondary successions—*Continued.*
    (4) In landslips.
    (5) In drained and dried-out soils.
    (6) By animal agencies.
    (7) By human agency.
      a. Burns.
      b. Lumbering.
      c. Cultivation.
      d. Drainage.
      e. Irrigation.
II. Anomalous successions.

With reference to the initial physical or biological cause, a normal succession was defined as one which begins with a bare area and ends in a climax, while anomalous succession was defined as that in which an ultimate stage of a normal succession is replaced by another stage, or in which the direction of movement is radically changed. The former was stated to be of universal occurrence and recurrence; the latter operates upon relatively few ultimate formations. Anomalous successions were regarded as the usual result of a slow backward-and-forward swing of climatic conditions. Primary successions were defined as those that arise on newly formed soils, or upon surfaces exposed for the first time. Such areas have in consequence never borne vegetation before. They present extreme conditions for ecesis, and possess few or no dormant disseminules. Accordingly, primary successions take place slowly and exhibit many stages. Secondary successions arise on denuded

soils, except in cases of excessive erosion. Denuded soils as a rule offer optimum conditions for ecesis, as a result of the action of the previous succession; dormant seeds and propagules are abundant, and the revegetation of such habitats takes place rapidly and shows relatively few stages. The great majority of secondary successions owe their origin to fire, floods, animals, or the activities of man. They agree in occurring upon soils of relatively medium water-content, which contain considerable organic matter and a large number of dormant migrants.

Successions were also classified as *imperfect, continuous, intermittent, abrupt,* and *interpolated* upon the basis of the nature of development. Initial causes were classified as (1) weathering, (2) erosion, (3) elevation, (4) subsidence, (5) climatic changes, (6) artificial changes. The reactions of succession were summarized as (1) by preventing weathering; (2) by binding aeolian soils; (3) by reducing run-off and preventing erosion; (4) by filling with silt or plant remains; (5) by enriching the soil; (6) by exhausting the soil; (7) by accumulating humus; (8) by modifying atmospheric factors. It was further stated that a natural classification of successions will divide them first of all into normal and anomalous. The former fall into two classes, primary and secondary, and these are subdivided into a number of groups, based upon the cause which initiates the succession.

Normal and anomalous succession.—The persistent study of successional development for the decade since the preceding views were enunciated seems to have confirmed and emphasized the distinction between normal and anomalous succession. Normal succession is unit succession, that is, the development from an initial bare area to a climax. It is represented by the sere, with its distinctions of prisere and subsere. Anomalous succession may be termed compound succession, *i. e.,* that in which similar or related seres are combined into a cosere as a consequence of climatic action. It is represented by the cosere and clisere, and in its major expression by the great successions of geological eras, the eoseres. Since climate rarely if ever produces a denuded area of any extent, the earlier distinction of normal and anomalous successions conforms closely to the present division into seres and cliseres. The former are essentially topographic or biotic as to cause, the latter are fundamentally climatic. Cowles (1911:170) has also recognized the validity of this distinction in contrasting climatic or regional successions with topographic and biotic ones.

Primary and secondary succession.—Further investigation appears to show conclusively that the distinction between primary and secondary seres is the outstanding fact of the development of existing formations. It is inherent in the organic nature of the formation (Chapter I), and is no more subjective than the reproduction by seed and propagation by offshoots in the case of an individual plant. The original distinction was somewhat confusing, as it placed too much weight upon the initiative process. In the case of erosion it was particularly difficult to determine offhand whether the new area was primary or secondary. The concept has now been definitized by basing it wholly upon development, though this basis necessarily includes reaction and the general influence of the denuding agent. From the developmental viewpoint, primary and secondary seres are wholly distinct. There is little or no possibility of confusing one with the other. At the same time

it must be recognized that a secondary sere may occasionally resemble a primary one very closely upon casual inspection. In rare cases, they can be distinguished only by the fact that the prisere has the pioneer stage, while the subsere begins with a late initial or subpioneer stage. Such instances are very rare, however, and in the vast majority of cases a subsere begins with a medial or subfinal stage. This occasional approximation of prisere and subsere is not an argument against the validity of the concept. In the individual plant an exact parallel is found in the case of species which replace the reproductive seeds wholly or in part by propagative bulbils, the development of the individual being all but identical in the two cases.

Cowles (1911:167) states that the classification into primary and secondary successions "seems not to be of fundamental value, since it separates such closely related phenomena as those of erosion and deposit, and places together such unlike things as human agencies and the subsidence of land." This objection brings out clearly the difference between the physiographic and the developmental views of vegetation. The former apparently makes physiographic distinctions paramount, while the latter regards development as the sole arbiter of the importance or value of any concept or principle. It has repeatedly been shown (Chapter II) that, while erosion and deposit are closely related physiographic processes, they are not closely related successional phenomena. Successionally they are indeed usually antagonistic, giving rise to fundamentally different bare areas. On the other hand, they may occasionally be equivalent as initial causes, producing xerophytic sand areas at one extreme or hydrophytic swamp areas at the other. In the life-history of a river the erosion of upland is obviously related to deposition in lowland, since the material for the one comes from the other. It is clear that no such relation exists between the two areas in so far as succession is concerned. Erosion on the upland yields regularly a xerarch sere, deposition on the lowland a hydrarch sere. The two seres may show a developmental relation by terminating in the same climax, or they may belong to wholly different formations. In either case, it is evident that the student of development is concerned with erosion and deposit only because, like a host of other agents, they produce initial bare areas for invasion.

Furrer (1914:30) has criticized the distinction into primary and secondary succession as a "far-reaching division, based predominantly upon deductive reasoning, and supported by insufficient analysis derived from practical experience." He further regards it as questionable whether the field ecologist can ever fall in line with this classification. This objection seems immaterial in view of what has been said in the preceding paragraph. Moreover, Furrer's experience in successional investigation is so very slight that little weight can be given his opinion of a developmental relation which has had more rigorous and extensive field tests than any other developmental concept except succession itself.

Roberts (1914:432) concludes that:

"The terms initial and repetitive seem to be better than primary and secondary in conveying the idea of often-repeated successions such as are found in a frequently deforested area. (443)

"It is doubtful if there is any climax representing that of the so-called primary succession, which might well be called the initial succession. The

region represents a third or fourth attempt to develop a climax forest, as do most of the New England forest areas. These successions have been called secondary successions, but might better be called repetitive associations, because the deforestation causes the area to revert to an aspect which is a combination of a former succession with the successions which ordinarily follow it. The term 'secondary' does not carry with it the idea of more than one attempt at repetition, while repetitive carries with it no limit in the number of attempts.'' (435)

These suggestions afford a striking illustration of the danger of generalizing upon the basis of a first study and that made upon a very limited area. The superficial fact of repetition is taken as more important than the process of development itself. It is not even recognized that ''initial'' or primary successions are repeated again and again in the same climax, as well as in the same spot. Moreover, the figure on page 442 indicates that there is no essential difference between the stages of burn ''repetitive'' and ''initial'' successions, a conclusion wholly impossible under the terms of an exact quantitative study.

Warming (1896:350) had already distinguished between changes in vegetation due to (1) the production of new soil and (2) changes in old soil, or in the vegetation covering it, particularly those caused by man. While this is not the full or exact distinction between primary and secondary succession, it does include much of it. The same idea is more clearly brought out in his earlier distinction (1892) between primary and secondary formations, in which the latter comprise those due to the influence of man. Tansley (1911:8) and his colleagues have used this concept of primary and secondary processes in connection with the study of succession in British vegetation. It has been adopted in America by Shantz (1906:187), Jennings (1908:291; 1909:306), Schneider (1911:290), Dachnowski (1912:223, 257), Gates (1912, 1915), Cooper (1913:11), Negri (1914:14), Pool (1914:304-306), Bergman and Stallard (1916) and others.

Cowles's system.—Cowles (1911:168) has classified successions as (1) regional, (2) topographic, and (3) biotic. He states that:

''In succession, we may distinguish the influence of physiographic and of biotic agencies. The physiographic agencies have two aspects, namely, regional (chiefly climatic) and topographic. (168) In regional successions it would seem that secular changes in climate, that is, changes which are too slow to be attested in a human lifetime, and which perhaps are too slow to be attested in a dozen or a hundred lifetimes, are the dominating factors. Regional successions are so slow in their development that they can be studied almost alone by the use of fossils. It is to be pointed out that great earth-movements, either of elevation or subsidence, that is, the far-reaching and long-enduring epeirogenic movements, as contrasted with the oscillations of coast-lines, must be considered in accounting for regional successions; the elevation of the Permian and the base-leveling of the Cretaceous must have played a stupendous part in instituting vegetative change. (170)

''In striking contrast to secular successions, which move so slowly that we are in doubt even as to their present trend, are those successions which are associated with the topographic changes which result from the activities of such agents as running water, wind, ice, gravity, and vulcanism. In general, these agencies occasion erosion and deposition, which necessarily must have a profound influence upon vegetation. As might be expected, the influence of

erosion generally is destructive to vegetation, or at least retrogressive, while the influence of deposition is constructive or progressive. (170)

"Of less interest, perhaps, to the physiographer than are the vegetative changes hitherto considered, but of far greater import to the plant geographer, are the vegetative changes that are due to plant and animal agencies. These are found to have an influence that is more diversified than is the case with physiographic agencies; furthermore, their influence can be more exactly studied, since they are somewhat readily amenable to experimental control, but particularly because they operate with sufficient rapidity to be investigated with some exactness within the range of an ordinary lifetime. If, in their operation, regional agencies are matters of eons, and topographic agencies matters of centuries, biotic agencies may be expressed in terms of decades. (171)

"At first thought, it seems somewhat striking that far-reaching vegetative changes take place without any obvious climatic change and without any marked activity on the part of ordinary erosive factors. Indeed, it is probably true that the character of the present vegetative covering is due far more to the influence of biotic factors than to the more obvious factors previously considered. So rapid is the action of biotic factors that not only the climate, but even the topography may be regarded as static over large areas for a considerable length of time. It has been said that many of our Pleistocene deposits exhibit almost the identical form which characterized them at the time of their deposition, in other words, the influence of thousands of years of weathering has been insufficient to cause them to lose their original appearance. These thousands of years would have sufficed for dozens and perhaps for hundreds of biotic vegetative cycles. Many a sand dune on the shores of Lake Michigan is clothed with the culminating mesophytic forests of the eastern United States, and yet the sand dunes are products of the present epoch; furthermore, sand is regarded generally as a poor type of soil in which to observe rapid succession. If a clay upland were denuded of its forest and its humus, it is believed that only a few centuries would suffice for the mesophytic forest to return. (172)

"Although they grade into one another as do all phenomena of nature, we may recognize climatic agencies, which institute vegetative cycles whose duration is so long that the stages in succession are revealed only by a study of the record of the rocks. Within one climatic cycle there may be many cycles of erosion, each with its vegetative cycle. The trend of such a cycle can be seen by a study of erosive processes as they are taking place to-day, but the duration of the cycle is so long that its stages can be understood only by a comparison of one district with another; by visiting the parts of a river from its source to its mouth, we can imagine what its history at a given point has been or is to be. Within a cycle of erosion there may be many vegetative cycles, and among these there are some whose duration is so short that exact study year by year at a given point makes it possible to determine not only the trend of succession, but the exact way in which it comes about. It is clear therefore that vegetative cycles are not of equal value. Each climatic cycle has its vegetative cycle; each erosive cycle within the climatic cycle in turn has its vegetative cycle; and biotic factors institute other cycles, quite independently of climatic or topographic changes." (181)

In the last two statements Cowles has made evident one of the chief objections to a primary classification of successions as regional, topographic, and biotic. This is that these successions actually represent three totally different degrees of development or developmental sequences. His biotic

succession is a developmental unit, a unit succession or sere; the topographic succession is a series of biotic successions, *i. e.*, a cosere; and the climatic cycle or succession is a series of coseres, *i. e.*, a clisere or an eosere. This reveals the basic objection to a classification grounded upon causes. As is obvious, it not only obscures the developmental subordination of the three kinds of succession, but it also ignores the fact that so-called biotic successions may be caused by topography, climate, or artificial agents, man, and animals. These may also be agents in topographic succession as well, though less frequently. As has been often pointed out in the discussion of initial causes, the same sere or cosere may result from a number of different causes. Moreover, climatic and topographic factors are inextricably mingled in the causation of eosere and clisere. This is inevitable from the coincidence of deformational, sun-spot and volcanic cycles (cf. "Plant Succession," fig. 26 and plate 57). Furthermore, in all periods with peat or coal seres and coseres, such as the Pleistocene, Cretaceous, Pennsylvanian, etc., the same development may result from flooding due to increased rainfall or to a local sinking of the region.

Another source of confusion lies in the fact that biotic succession is stated to be due to plants and animals. The rôle of plants is that of reaction upon the habitat, as a consequence of which one stage succeeds another. Such a reaction is typical of all succession, and the latter would be impossible without it. Man and animals, on the contrary, are initial causes, as is topography, and have little to do with reaction. Hence, as already shown (Chapter III), it is imperative for the understanding of vegetational development to distinguish initial causes, topographic, climatic, and biotic, from ecesic or continuative causes, of which reaction is the most striking. Moreover, a plant may itself be an initial cause, in such instances as the one mentioned, where *Cuscuta* produced a bare area again by completely destroying the pioneers of a dune sere. This confusing double use of the term biotic is well illustrated by the statements of Paulsen (1912:104) and Matthews (1914:143). Speaking of the sand desert, Paulsen says that the development from stable to unstable desert through the agency of man must be considered a biotic succession. Matthews, in describing the water sere in Scotland, states that there seems to be sufficient evidence for regarding the main determining factors as entirely biotic. In the former, the cause of the bare area is biotic, in the latter, topographic; in both the ensuing course of development is due to the reaction of plants, and is necessarily biotic.

Crampton (1911:20; 1912:4) has adopted Cowles's classification, as have also Crampton and MacGregor (1913:180), but his application of the terms appears to be more or less divergent. The regional successions of Crampton seem to include the small and recent swings of climate, such as are found in the coseres of peat-bogs (1911:22), rather than the great eoseres of geological history. His topographic successions seem to be the existing ones due to local topographic initial causes (1911:29) and not those of Cowles, which are related to the vast regional changes comprised in an erosion cycle. Crampton appears to ignore biotic successions altogether, especially the vast number of secondary successions, regarding the local topographic succession as well-nigh universal, while Cowles ascribed much the greater importance at present to his biotic successions (1911:172). Crampton's treatment is still further com-

plicated by the distinction between stable or paleogeic and migratory or neogeic formations, which seem to correspond roughly to climax and seral communities respectively. It also serves to lend much emphasis to the fact that in the study of the development of vegetation, development is obviously paramount and physiography quite secondary.

Watson's (1912:213) use of the term "biotic succession" also illustrates the inevitable confusion to which it leads:

"After a fire in the Douglas spruce, the quaking aspen always takes possession, but it has also its natural place as a transition between the oak chaparral and the Douglas spruce in the biotic succession. The biotic succession in the Sandia Mountains is as follows: The bare rock first incrusted with crustose lichens, then foliose lichens, mosses, herbs, oaks, followed in some cases directly by Douglas spruce, and in others by aspen and then the spruce; and then as physiographic succession comes in, the poplars, pines, and box-elders in the cañon and pine, piñon, and cedar on the slopes, and the ultimate formation of the mesa is reached."

The aspen is a characteristic stage of the secondary succession due to man as a biotic cause, while it progresses to the Douglas-spruce stage in consequence of the reactions of plants as biotic agents. The last is also true of the primary succession initiated on rock by crustose lichens, but as to cause, this succession is essentially topographic.

Siegrist (1913:145) has also distinguished topographic and biotic successions, but his topographic succession is the biotic succession of Cowles. This is shown by the definition of a topographic succession as one in which a topographic change is necessary for the initiation of a new formation. The examples given on pages 158 and 159 further prove that he is concerned with local unit succession or seres, and not at all with the topographic successions of Cowles, which are matters of centuries and belong to far-reaching erosive cycles. Biotic succession is defined as one in which no topographic change is necessary, though it does not exclude the simultaneous occurrence of such changes, which, however, have no influence upon the biotic succession. The author's use of the term is in itself incorrect as well as misleading, as he employs it for parts of a unit succession or sere (*l. c.*, 145, 158), *e. g.*, Hippophaëtum——>Pinetum, Hippophaëtum——>Transition association, Pinetum——>Transition association. As already indicated, his topographic associations are necessarily biotic in reaction, and would be called biotic successions by Cowles. The distinction made on page 159 is far from evident, but it seems to be based upon whether colonization takes place in the water or upon a new area of sand or gravel. From the standpoint of development, a pond or stream is just as much a bare area due to a topographic initial cause as is a sand-bar or a gravel-bank, and the succession on each proceeds as a consequence of the biotic reactions of the plants. It is also difficult to understand how local topographic changes can occur without initiating or affecting succession.

Dachnowski (1912:259) has distinguished two kinds of successions, as follows:

"Two great, relatively wave-like and integrating phases of vegetation successions define themselves rather clearly: (1) the climatic successions, associated with the succession of geological periods and of which the migration of

plants accompanying and following the retreat of the glaciers is an example; (2) the edaphic successions, in which the replacement of one type of vegetation by another has resulted from changes in topography and a bio-chemically diminished water-supply."

The climatic successions are the regional successions of Cowles, and the edaphic ones correspond partly to his topographic and partly to his biotic successions, thus emphasizing the impossibility of distinguishing between the two on the grounds proposed. Dachnowski's climatic successions would include the geosere, eoseres, and cliseres and coseres in part, though deformation and gradation play a profound rôle in them. His edaphic successions would correspond partly to the cosere and sere. According to the definition given, seres due to biotic initial causes would find no place in either group. In short, the distinction proposed, like all of those based upon initial causes, runs counter to the process of development, and hence is largely artificial.

Braun and Furrer (1913:19) use the term *phylogenetic successions* for the regional successions of Cowles, though this term should obviously include his topographic successions as well. Contrasted with this is the ontogeny of actual communities, which establish themselves under the eyes of the observer. These apparently correspond exactly to the biotic successions of Cowles, though the authors ignore this fact, and distinguish *artificial successions,* equivalent to Cowles's retrogressive biotic successions.

Possible bases of classification.—From the preceding discussion it becomes clear that development, cause, initial area, and climax must be weighed as possible bases for the classification of successions. Reaction is not available, since one sere is often the result of several reactions, and since widely different seres may have the same sequence of reaction. Since the reaction upon water-content is nearly universal in succession, classification may be based upon the direction of movement, such as mesotropic, xerotropic, etc., but our present knowledge hardly suffices for this.

In a natural, *i. e.,* a developmental system of classification, it is clear that development must constitute the chief basis. This is true of the actual seres of to-day, which culminate in the present climax formation. It is true of the cliseres, which result from the shifting of existing climaxes, and of the coseres formed by successive seres. It is even more marked in the eoseres, which are major developmental series within the climatic climax of the geological eras. In short, seres are related to each other by their development into the same climax and by their sequence in the cosere. Climaxes, the static units of to-day, are related to each other in the developmental sequence of the clisere, which is produced by a change of climate, such as glaciation. These climaxes of the existing flora are phylogenetically the descendants of the climaxes of a preceding flora, which characterized an eosere. All eoseres have a similar phylogenetic relationship, and taken together constitute the geosere, the whole course of the development of vegetation from its beginning down to the present.

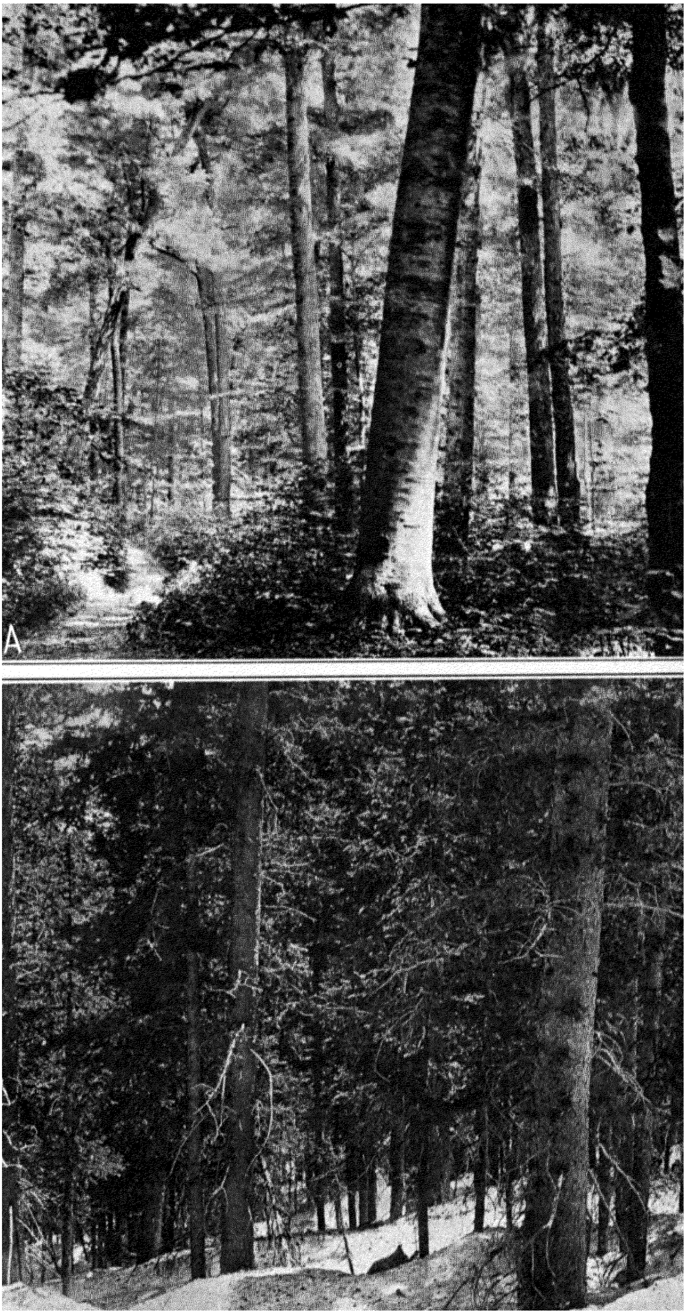
Developmental basis of classification.—While the unique importance of development for successional analysis and classification has repeatedly been emphasized, it is felt that over-emphasis is impossible. Though it is easy to carry analogy too far, there seems to be no question that the history of ecology must repeat that of botany itself to a large degree. In morphology and tax-

onomy, development alone is regarded as capable of furnishing basic criteria, and the great advances in these fields are regarded as necessarily consequent upon an increased knowledge of development. What is true of the individual and the species seems equally true of the community. Studies of physiognomy, floristic, and habitat all have their importance, but their chief value lies in their correlation into the basic process by which communities arise and grow, namely, development. It is evident that our knowledge of development will advance more slowly than it will in the three fields just mentioned, but it is also clear that the final importance of any advance will depend upon its developmental significance.

The natural classification of seres rests upon the fact that each sere leads to a climax or formation. Hence, the fundamental grouping of seres is determined by their relationship to a particular formation. As a consequence, all the seres of one formation constitute a natural group, strictly homologous with all the seres of another formation. Thus, all the existing seres of the world fall into as many coordinate groups as there are climatic climaxes in vegetation. In short, the primary division in a natural classification of seres is that into climaxes or formations. As previously indicated, the latter fall into the major developmental groups of clisere and cosere. While formations may also be arranged in formation groups, classes, or types, for convenience of reference, such groupings seem unfortunate in that they tend to postpone a natural classification (plate 21, A, B).

The grouping of seres within each formation should also be based upon development. The reasons for the distinction of primary and secondary seres have been discussed at length (pp. 60, 169), and it is only necessary to emphasize the fact that these represent the basic developmental differences within the formation. The actual recognition of priseres and subseres is a simple matter, except occasionally in the final stages which are converging into the climax. The distinction between primary and secondary bare areas is readily made as a result of experience in successional investigation, though it should always be checked by instrumental study. The only possible difficulty with the division into prisere and subsere arises when the secondary disturbance is so profound as to cause the resulting area to approach the condition of a primary one. The difficulty here, however, is not one of distinguishing prisere and subsere, since the distinction between them is clear-cut. The prisere repeats the whole course of normal development, the subsere retraces only a part of it. The subsere regularly comprises the later half or less of the succession. While it may exceptionally begin at an earlier point, its initial stage is always subsequent to the pioneer associes of the prisere. In short, a subsere can never begin on an initial bare area of rock, water, or sand unless the effects of plant reaction are already manifest in it.

Initial areas and causes.—It has already been shown that the significance of initial areas for succession lies in the conditions as to water-content, and not in their causes. Since the initial water-content is determined in some degree by the initial cause, the latter may be used as the basis for subdivisions. In this connection, however, it is necessary that the causes themselves be considered and grouped from the standpoint of their effect upon water-content, and not from that of their nature. Such a classification would regularly separate erosion and deposit by water, since the one produces relatively dry and



A. Deciduous forest climax of *Acer-Fagus*, Three Oaks, Michigan.
B. Subalpine forest climax of *Picea-Abies*, Mount Blanca, Colorado

the other relatively wet initial areas. It would bring them together when they produce essentially the same area, as is frequently true of wind erosion and deposit, and not altogether rare in the case of water. While the value of the initial area for purposes of classification rests upon its water-content, it must not be forgotten that the nature of the latter may be more significant than its amount. In other words, an alkaline or acid holard may determine the nature of the sere, more or less irrespective of the amount of water present.

The initial causes of bare areas are largely or predominantly physiographic. Their rôle in succession is not due to their nature as physiographic processes, but to their effect upon water-content. As indicated above, this effect is due in some degree, and often a controlling one, to the nature of the agent. This relation is not so definite, however, that the process can be substituted for water-content as a basis of classification. Thus, while it is clear that a complete study of succession must include the causes which initiate seres, it assigns to physiography a subordinate rôle in classification as in development.

Relative importance of bases.—The basic division of the developmental classification of seres here proposed is the climax or formation. Every climax is subdivided into priseres and subseres, each with a larger or smaller number of adseres. Priseres and subseres are further grouped with reference to the initial water-content of the bare area, in the manner indicated by Cooper's distinction into hydrach and xerarch seres. Finally, these may be further divided into groups based upon the causes which produce a particular bare area. Such a classification is developmental throughout, since even the minor divisions based upon initial causes have this value, if the causes are grouped in accordance with their action rather than their nature.

The climax as a basis.—The nature of the climax as the final condition of the vegetation of a climatic region through a climatic period makes unavoidable its use as the primary basis for the classification of existing seres. The use of the climax necessarily depends upon its recognition, and this is a matter of some difficulty in the present state of our knowledge. Neither climatology nor ecology has reached a point at which climatic climaxes can be delimited accurately. In fact, climatology is obviously of secondary importance in this connection. While it is perhaps easier to study climate than vegetation, it is the latter alone which makes possible the recognition of a particular climate so far as plants are concerned. In other words, a climax must be determined by its developmental and structural character, as is true of any biological unit. This is true in spite of the fact that climate is the cause of a climax, or at least the force in control of it.

In the United States and Europe the developmental study of vegetation has gone far enough to disclose a large number of seres. This has had the effect of delimiting in a general way the majority of climaxes on the two continents, first by determining the successional termini of the various regions, and secondly, by making it possible to distinguish between seral stages, associes and consocies on the one hand, and ultimate communities, associations and consociations on the other. The result has been to confirm the general floristic evidence as to the existence and extent of climaxes, though the limits and relations of these are still to be determined with precision.

Recognition of climax areas.—All the attempts to divide the surface of the earth into vegetation zones or climatic regions have some bearing upon

the problem of climax areas. The various divisions of North American vegetation by Gray (1878), Engler (1879), Sargent (1880), Drude (1887), Merriam (1898), Clements (1904), Harshberger (1911), and others, have either been based more or less completely upon the basic climax units, here regarded as formations, or at least represent them in some degree. Thus, while there is the usual divergence of view as to the basis, relationship, and terminology of the various subdivisions, there is necessary agreeement as to the actual existence of a more or less definite number of distinct vegetation areas. Few attempts have been made to investigate these as climaxes and to determine their limits, relations, and development. Cowles (1899, 1901) and Whitford (1901) have considered the general relation of development to climax in the forested region of Illinois and Michigan. Adams (1902:128) has sought to lay down general rules for the study of life centers, in connection with a study of the southeastern United States as a center of dispersal and origin:

"First. In general the fauna and flora of northern United States east of the Great Plains are geographically related to those of the Southeast and this geographical relationship points to an origin in the direction of the Southeast except in the case of the distinctly boreal forms.

"Second. The abundance and diversity of life in the Southeast indicate that it has been, and now is, a center of dispersal.

"Third. The relicts indicate that the Southeast has been a center of preservation of ancient types, and the endemism shows that it has been a center of origin of types.

"Fourth. There are two distinct southern centers of dispersal in temperate United States; one in the moist Southeast, and the other in the arid Southwest.

"Fifth. Ten criteria, aside from fossil evidence, are recognized for determining the center of origin or the locality of dispersal:

"1. Location of the greatest differentiation of a type.
"2. Location of dominance or great abundance of individuals.
"3. Location of synthetic or closely related forms. (Allen.)
"4. Location of maximum size of individuals. (Ridgway, Allen.)
"5. Location of greatest productiveness and its stability, in crops. (Hyde.)
"6. Continuity and convergence of lines of dispersal.
"7. Location of least dependence upon a restricted habitat.
"8. Continuity and directness of individual variations or modifications radiating from the center of origin along the highways of dispersal.
"9. Direction indicated by biogeographical affinities.
"10. Direction indicated by annual migration in birds. (Palmén.)

"Sixth. There are three primary outlets of dispersal from the Southeast:

"1. The Mississippi Valley and its tributaries.
"2. The Coastal Plain.
"3. The Appalachian Mountains and adjacent plateaus.

"The first two have also functioned for tropical types, and the third for boreal forms. Dispersal is both forward and backward along these highways.

"Seventh. The individual variations of animals and plants, such as size, productiveness, continuity of variation, color variation, and change of habit and habitats, should be studied along their lines of dispersal and divergence

from their center of origin. Life areas should be studied as centers of dispersal and origin, and hence *dynamically* and *genetically.*"

In studying the forest vegetation of eastern America by plotting the ranges of dominant trees, Transeau (1905:886) confirms the results of earlier observers as to the existence of four distinct forest centers, namely:

"(1) The Northeastern conifer forest centering in the St. Lawrence basin, (2) the deciduous forest, centering in the lower Ohio basin and Piedmont plateau; (3) the Southeastern conifer forest, centering in the south Atlantic and Gulf Coastal plain; and (4) the insular tropical forest of the southern part of the Florida peninsula, centering in the West Indies. The term center, as here used, implies the idea of distribution about a region where the plants attain their best development. Such vegetation divisions are not fixed, but move and increase or decrease in extent depending upon continental evolution and climatic change.

"It has been found that if the ratios, produced by dividing the amount of rainfall by the depth of evaporation for the same station, be plotted on a map, they exhibit climatic factors which correspond in general with the centers of plant distribution. Further, the distribution of grassland, prairie, open forest, and dense forest regions is clearly indicated. This is explained by the fact that such ratios involve four climatic factors, which are of the greatest importance to plant life, viz, temperature, relative humidity, wind velocity, and rainfall."

Recently, Livingston (1913:257) has integrated the temperature and moisture relations of the climatic areas, and has developed a general method of determining the climatic control of climax formations. We are still far from the final method for delimiting climaxes and their climates. It seems clear, however, that it must be based primarily upon the range of consociations, and upon the measurement of the growth and reproduction of their dominants in relation to the water and temperature conditions of both the growing and resting periods.

Climaxes of North American vegetation.—Clements (1902:15; 1904:160) has made an analysis of North American vegetation upon the basis of temperature and water zonation, in an endeavor to determine the great vegetation centers. The major continental zones were thought to be due to temperature and water, and their interruption to the decreasing rainfall and increasing evaporation toward the interior, as well as to the disturbing effect of mountain ranges. The 17 provinces were supposed to indicate as many vegetation centers, but they were determined floristically, by the superposition of the ranges of dominants, and not developmentally. Hence, while most of them correspond to climax formations, some obviously do not. With the recognition of the formation as the major unit of vegetation, the question of zones, regions, provinces, etc., becomes of minor importance. These are geographical distinctions based upon floristic, while the developmental method demands vegetation distinctions based upon climaxes and the course of succession.

The first division of the vegetation of North America into climax formations was made in "Plant Succession" (page 180) and was necessarily based upon field work done before 1915. It was recognized at that time that the existing knowledge permitted only a tentative outline, and in consequence especial attention was devoted to the recognition and *(continued on page 184)*

CLIMAXES OF NORTH AMERICA

GRASSLAND CLIMAXES:

Grassland: Stipa-Bouteloua Formation

1. True Prairie: Stipa-Sporobolus Association
   - 1a. Subclimax Prairie: Andropogon Associes
2. Coastal Prairie: Stipa-Andropogon Association
3. Mixed Prairie: Stipa-Bouteloua Association
   - 3a. Short-grass Plains: Bulbilis-Bouteloua Associes
4. Desert Plains: Aristida-Bouteloua Association
5. Pacific Prairie: Stipa-Poa Association
6. Palouse Prairie: Agropyrum-Festuca Association

Sedgeland (Tundra): Carex-Poa Formation

1. Arctic Tundra: Carex-Cladonia Association
2. Petran Tundra: Carex-Poa Association
3. Sierran Tundra: Carex-Agrostis Association

SCRUB CLIMAXES:

Sagebrush: Atriplex-Artemisia Formation

1. Basin Sagebrush: Atriplex-Artemisia Association
2. Coastal Sagebrush: Salvia-Artemisia Association

Desert Scrub: Larrea-Franseria Formation

1. Desert Scrub: Larrea-Franseria Association
   - 1a. Bronze Scrub: Larrea-Flourensia Associes
   - 1b. Mesquite: Acacia-Prosopis Associes
   - 1c. Sotol: Agave-Dasylirion Associes
   - 1d. Thorn Scrub: Cereus-Fouquiera Associes

Chaparral: Quercus-Ceanothus Formation

1. Petran Chaparral: Cercocarpus-Quercus Association
   - 1a. Oak-sumac Subclimax: Rhus-Quercus Associes
2. Coastal Chaparral: Adenostoma-Ceanothus Association

FOREST CLIMAXES:

Woodland: Pinus-Juniperus Formation

1. Piñon-juniper Woodland: Pinus-Juniperus Association
2. Oak-juniper Woodland: Quercus-Juniperus Association
3. Pine-oak Woodland: Pinus-Quercus Association

Montane Forest: Pinus-Pseudotsuga Formation

1. Petran Montane Forest: Pinus-Pseudotsuga Association
2. Sierran Montane Forest: Pinus-Abies Association

Coast Forest: Thuja-Tsuga Formation

1. Cedar-hemlock Forest: Thuja-Tsuga Association
   - 1a. Douglas-fir Subclimax: Pseudotsuga Consocies
2. Larch-pine Forest: Larix-Pinus Association

Subalpine Forest: Picea-Abies Formation

1. Petran Subalpine Forest: Picea-Abies Association
   - 1a. Lodgepole Subclimax: Pinus consocies
2. Sierran Subalpine Forest: Pinus-Tsuga Association

Boreal Forest: Picea-Larix Formation

1. Spruce-larch Forest: Picea-Larix Association
   - 1a. Birch-aspen Subclimax: Betula-Populus Associes
2. Spruce-pine Forest: Picea-Pinus Association

Lake Forest: Pinus-Tsuga Formation

1. Pine-hemlock Forest: Pinus-Tsuga Association
   - 1a. Jack-pine Subclimax: Pinus Consocies

Deciduous Forest: Quercus-Fagus Formation

1. Maple-beech Forest: Acer-Fagus Association
2. Oak-chestnut Forest: Quercus-Castanea Association
3. Oak-hickory Forest: Quercus-Hicoria Association
   - 1a. Pine Subclimax: Pinus Associes

Isthmian Forest

Insular Forest

SUBCLIMAXES:

The major advances made in the past fourteen years have consisted largely in the more exact delimitation of subclimaxes. At the time of the first treatment, it was still uncertain how much of the prairie proper was to be regarded as subclimax, though by 1920 it had become evident that the true prairie comprised the larger part of it. In the later arrangement, the short-grass plains were still treated as climax, but the study of relict and protected areas, and in particular of experimental exclosures, has demonstrated that they constitute a subclimax caused by grazing. The detailed investigation of climaxes in Texas has revealed a new association, the coastal prairie, related to both the subclimax and true prairies (Tharp, 1926; Clements and Tharp, 1926). Similarly, a more intimate acquaintance with the bunch-grass prairie of the Pacific Coast has made it desirable to divide this into the Pacific and Palouse prairies, owing to the fact that the chief dominants are different. Finally, the field experiments carried out in connection with "Experimental Vegetation" and "Plant Competition" have furnished objective values to these new viewpoints.

The understanding of the desert scrub has been greatly promoted by resident studies in Arizona and California during the last decade. The outcome has been the recognition of a single climax association characteristic of the desert climate of the lower Colorado Basin. With it are associated four subclimaxes, the first two being due primarily to overgrazing and fire and the last two related to rocky foothills and escarpments.

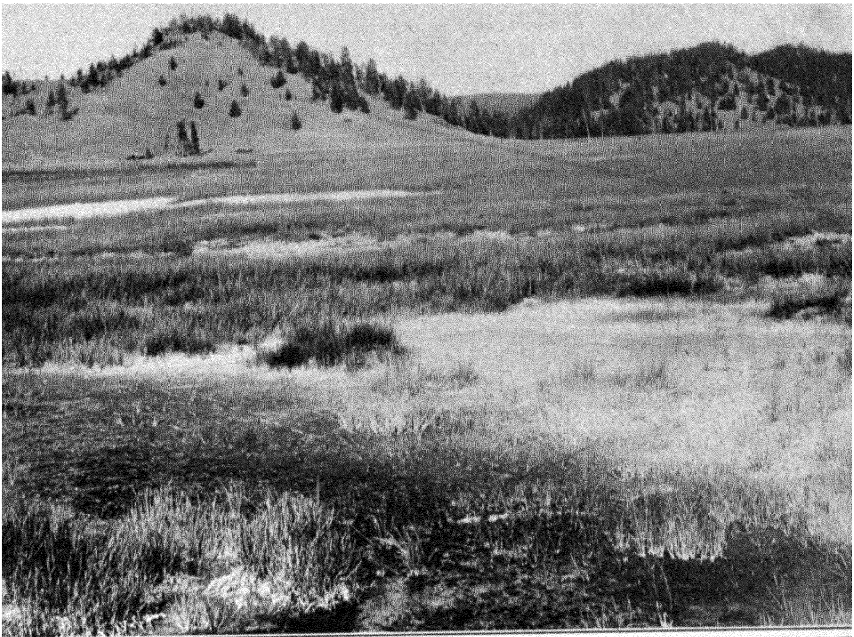
It is as significant as it is interesting to note that the chaparral and forest climaxes all exhibit subclimaxes, with the exception of woodland, a large part of which is itself subclimax today. The lodgepole subclimax is placed in the subalpine forest, but it also extends well into the zone of the montane forest.

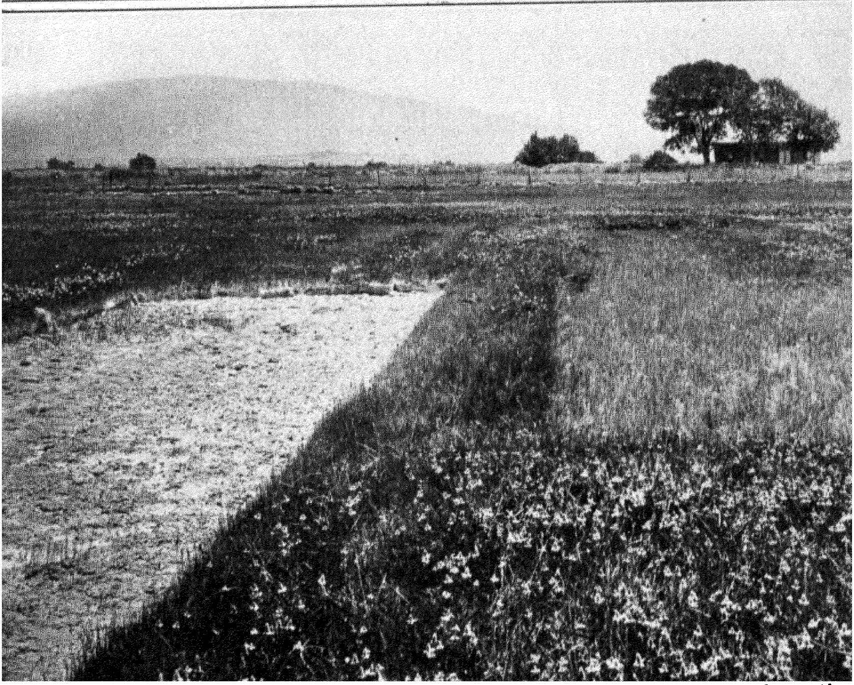
Names of climaxes.—A consistent endeavor has been made to render the nomenclature of formations and associations as simple, uniform and definite as possible. In the tentative arrangement first proposed it seemed desirable to prepare the way for an international nomenclature by means of technical terms for the two major divisions, such as *hylion* for a forest formation and *hylium* for an association. These terms still have distinct values and may come into more general use, as developmental studies become more or less universal. However, the use of the words formation and association is becoming more and more the rule, and this may well make the less familiar *hylion, dryon, poion,* etc., unnecessary.

The nomenclature exemplified in the present classification of climaxes is essentially binomial in character. Moreover, it comprises two sets of names, the one technical and adapted to international usage, the other vernacular and suited to more general purposes. The former are limited to the names of the two most important dominants, or even to a single one when the chief dominants belong to the same genus. The endeavor has been made to attain the optimum with respect to brevity, definiteness, uniformity, and attractiveness.

Extent and relationship of the climaxes.—The general position and extent of the climaxes of western North America have been indicated in Chapter IV of "Plant Indicators." They are exhibited graphically in the vegetation map of the United States by Shantz and Zon (1924), which is in close accord with the earlier classifications indicated above. Because of the practical needs of agriculture, grazing and forestry, the names of the communities follow more nearly the everyday usage in these fields, but the genera listed for each make it possible to refer the divisions of the map to the proper formations and associations.

Much progress has been made in the study of the phylogeny of the climaxes of the North American continent, both with respect to their relationship to each other and to the similar formations of Eurasia. It is even more evident than it was fifteen years ago that the phylogeny of climaxes must provide the key to an adequate understanding and treatment of them, such as is proposed in the books now under way or contemplated.





A. Prisere alternes showing the seral stages from the bare diatom marsh to the lodgepole subclimax, Firehole Basin, Yellowstone Park.

B. Subsere alternes due to the removal of sods for adobe houses, showing three stages: (1) rushes, (2) salt-grass, (3) *Anemopsis*, Albuquerque, New Mexico.

only for a portion of the sere. Moreover, while the surfaces of rock and of dune-sand may be almost equally dry, the differences of hardness and stability result in very dissimilar adseres. These may be distinguished as *lithoseres* (Gr. λίθος, rock) and *psammoseres* (Gr. ψάμμος, sand), or as *litharch* and *psammarch*. Finally, hydroseres and xeroseres may be also distinguished upon the basis of the agents concerned in producing bare areas. While this has value in connection with the origin of such areas, it is not fundamental, and hence is out of place in a developmental classification (plate 23, A. B).

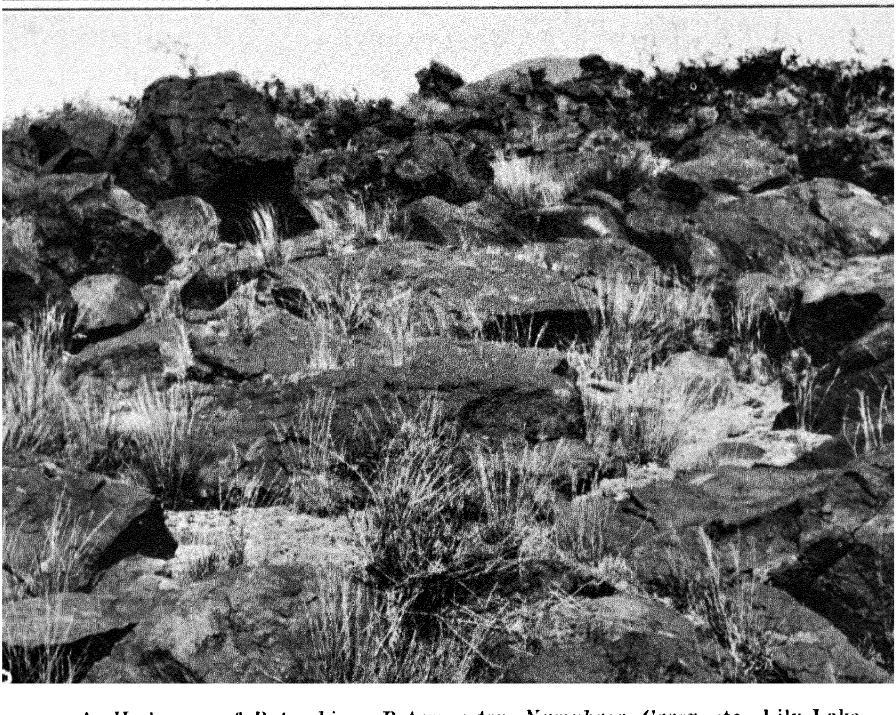
Phylogenetic system.—The arrangement proposed above deals with the grouping of seres within a particular climax. It applies to the relations of existing seres, as well as to those of each period or era and sums up the ontogeny of the climax formation. The phylogenetic relations of the latter obviously must be sought in the geological past. They serve to show the immediate origin of the climaxes of to-day, and to summarize the lines of vegetational descent in the remote past. The complete system of classification is shown in the accompanying outline.

- Geosere.
  - Eosere.
    - Clisere.
      - Cosere.
        - Sere (climax).
          - Prisere.
            - Hydrosere.
              - Halosere.
              - Oxysere.
            - Xerosere.
              - Lithosere.
              - Psammosere.
          - Subsere.
            - Hydrosere.
            - Xerosere.

X. THE INVESTIGATION OF SUCCESSION.

Primary methods.—There are three primary methods of investigating succession: (1) by inference; (2) by sequence, (3) by experiment. Investigation by inference consists in piecing together the course of development from the associes and consocies found in a region. From the very nature of succession, this method was necessarily the first one to be employed, and its use still predominates to the practically complete exclusion of the other two. This is easily understood when one recalls that it is the only method that can be applied in studies lasting but one or two seasons. Moreover, the interpretation of successional evidence has reached a point where inference often yields fairly conclusive results, and regularly furnishes the working hypotheses to be tested by the methods of sequence and experiment. In a complete system of investigation, inference can only furnish the preliminary outline, which must be subjected to thoroughgoing test by means of sequence and experiment before the course of succession can be regarded as established. However, it must be recognized that the value of inference, even when used alone, must steadily increase in just the degree that it is confirmed by the other two methods. Successional studies have been slow in making their way in ecology, in spite of their fundamental value, because of the labor and time demanded even by the method of inference. The adoption of the more conclusive and exacting methods of sequence and experiment will be slower still, but there would seem to be no serious doubt of their final and complete acceptance.

The method of sequence consists in tracing the actual development of one or more communities in a definite spot from year to year. In short, it is the direct study of succession itself as a process. It is clear that sequence must furnish the basic method of study, and that the value of inference and experiment depends upon the degree to which they reveal the sequence itself. If the whole course of development from bare area to climax required but a few years, or a decade or two at most, the method of sequence would give us a complete account of succession. But even the shortest of secondary seres require a decade or longer, and most of them demand more than the working period of a life-time. Primary seres rarely if ever complete their development within a century, and the large majority of them last through several centuries, or even millenia. As a result, the method of sequence can not be applied directly by a single investigator to the whole course of development from the pioneer colonies in water or on rock to the final grassland or forest climax. Three possible solutions present themselves, however. He may carry his studies of a particular community as far as possible, and then turn his records of the development over to a younger investigator, who will carry the record through another life-time. Such a method requires concerted action such as is unknown at present, but there can be little question that continuous investigations of this nature will soon be organized by great botanical institutions. In fact, an approach to it has already been made by the Desert Laboratory of the Carnegie Institution of Washington and by some of the experiment stations of the United States Forest Service. So far, however, research is chiefly a function of the individual investigator, and he will seek one or both of the



A. Hydrosere of *Batrachium*, *Potamogeton*, *Nymphaea*, *Carex*, etc., Lily Lake, Estes Park, Colorado.

B. Xerosere of lichens, mosses, annuals and grasses on lava ridges, Death Valley, California.

other solutions. The most obvious one is to make a simultaneous study of the development of what appear to be different stages of the same sere. In this way the whole course of succession may actually be traced in a few years by the same individual. The one difficulty lies in properly articulating the different portions thus studied, and here he must call inference to his aid, or, what is better, make a special synchronous investigation of the actual development between every pair of stages. As a matter of fact, intensive investigation of this sort makes it evident that he must avail himself of both sequence and experiment wherever possible. The complete method, then, begins with inference, but rests primarily upon sequence, reinforced to the highest degree by experiment.

The method of experiment is a highly desirable, if not an indispensable adjunct to the method of sequence. Its great value lies in the fact that it makes it possible to reproduce practically any or all portions of the course of development, and to keep them under intensive observation. Its use is imperative in climax areas which show few or widely scattered seral communities, while it greatly reduces the period necessarry to secure conclusive results in an area where developmental stages predominate, as in some mountain regions. It is especially dependent upon the quadrat method, and will be further discussed in that connection.

Special methods.—The special methods of successional investigation may be grouped under four heads, viz, (1) quadrat method, (2) mapping, (3) instrumentation, (4) recording. All of these are intensive in nature and in purpose, with the exception of large-scale mapping, and hence find their use in connection with the general methods of sequence and experiment. The quadrat method is the essential basis of them all, and may alone suffice for the study of development pure and simple. The latter can not be understood, however, without a thorough analysis of the habitat and the plant reactions upon it, and for such work instruments are indispensable. Moreover, much ecological work has failed of its purpose for the lack of an adequate method of record. Such a record becomes all the more imperative with the increase of intensive investigation, and it must soon come to be recognized that no successional study is complete without a detailed record of observation and experiment. This record should be wholly separate from its interpretation, a result which can be secured only by the impersonal methods of quadrating and instrumentation. Mapping is primarily a method of record, but it is also possible to use it in connection with quadrat and instrument for purposes of investigation.

THE QUADRAT METHOD.

Concept and significance.—The quadrat method is regarded as comprising all the exact methods of determining the composition and structure of plant communities, irrespective of the shape or size of the measure. While no definite line can be drawn between methods of quadrating and mapping, the latter is here considered to be upon a scale which does not permit dealing with individuals, and hence mapping must confine itself to the distribution and relations of communities. It is clear that the two may be used conjointly in the same area and combined in the final record, as is shown later in the methods employed by the Botanical Survey of Minnesota. While this basic method of successional study is named from the most important measure, the quadrat,

it includes also the transect, bisect, and migration circle. Though all of these differ in form and to some degree in purpose, they are alike in being based upon the enumeration or charting of the individuals of a community within a circumscribed area, and in disclosing as well as registering the changes in population and structure which are the record of development.

The use of squares for purposes of enumeration or of determining the amount of plant material produced has occurred occasionally for a century or more (Sinclair, 1826; Darwin, 1859; Hanstein, 1859; Blomquist, 1879; Stebler and Schröter, 1883-1892; etc.; *cf.* Schröter, 1910:117). It was organized into a definite system for the study of the structure and development of vegetation by Pound and Clements (1898[2]:19; 1900:61) and Clements (1904; 1905:161; 1907:202; 1910:45; *cf.* also, Thornber, 1901:29). It has since been used by Sernander (1901), Jaccard (1901), Oliver and Tansley (1905), Shantz (1906, 1911), Young (1907), Sampson (1908, 1915), Spalding (1909), Raunkiaer (1909), Gleason (1910), Howe (1910), Tansley (1911), Pallis (1911), Adamson (1912), Cooper (1913), Priestley (1913), Kearney (1914), Pool (1914), Weaver (1914, 1915), Hofmann (1916), Bergman and Stallard (1916), and others. With the rapid increase in the number of successional studies, the use of the quadrat and its modifications may be expected to become as universal as it is fundamental.

Kinds of quadrats.—Quadrats are distinguished with respect to their purpose, location, or size. From the standpoint of purpose and use, they are divided into list, chart, permanent, and denuded quadrats. As to their location in a community or kind of community, they are known as layer, soil, water, lichen, moss quadrats, etc. The unit quadrat is taken as 1 meter square. This may be divided into subquadrats of a decimeter or a centimeter square, or grouped into perquadrats up to 100 or even 1,000 meters square. The meter quadrat is the unit for herbland, herbaceous layers, and grassland, the 10-meter for scrub, and the 100-meter for forest. List quadrats are chiefly useful for taking a census of individuals, species, or life-forms, and making floristic comparisons. Chart quadrats are primarily to record composition and structure, while permanent and denuded quadrats are especially designed for the study of succession by the methods of sequence and experiment.

List quadrat.—The list quadrat is of slight value for the study of succession, since the latter demands the actual study and record of a definite area from year to year. It serves for the superficial values of reconnaissance, but is of small use for intensive investigation. Its chief interest lies in the fact that it was the pioneer quadrat method, and that it has given rise to two applications, which have met with some favor. These are the methods of Jaccard and of Raunkiaer, both designed to permit a more exact comparison of localities, communities or regions upon the basis of floristic, and of physiognomy also, to a certain extent. Jaccard (1901, 1902, 1908, 1912, 1914) has made use of the list quadrat to establish a statistical method for floristic, with especial reference to the origin of the flora of a region. His method is based upon: (1) the *coefficient of community*, or the degree of similarity of composition between the different portions of the same region; (2) the *degree of frequence* of each species; and (3) the *generic coefficient*, or the percentage relation of the number of genera to the number of species (*cf.* Drude, 1895:17; Pound and Clements, 1900:59, 63). The application of Jaccard's principles to pres-

ent-day succession is difficult if not impossible, but it will perhaps serve as a valuable aid in tracing the differentiation of the flora of an era into climaxes, and the migrations of genera and species during a clisere. To serve this purpose, however, it must be modified to take account of existing differences of composition and structure due to development.

Raunkiaer (1905; 1910:171; *cf.* Smith, 1913:16) has established a new system of life-forms or growth-forms based primarily upon the nature and degree of bud protection during the unfavorable season of the year. The author justly regards the use of a single criterion as more satisfactory in that it permits definite comparisons, and enables one to correlate life-forms and climate much more accurately. The analysis of the flora of any region into its life-forms gives a *biologic* or *phyto-climatic spectrum,* which is compared with a theoretical norm called the *normal spectrum.* This method is also applicable in some degree to communities in connection with Raunkiaer's use of the list quadrat (1909:20), later modified into a circle (1912:45). This has the advantages and disadvantages of the list quadrat, but its chief drawback lies in its failure to take account of succession. Its values are floristic alone, and the intensive worker will quickly pass to the more thoroughgoing methods of quadrating.

Chart quadrat.—Chart quadrats differ from permanent and denuded ones which are also recorded in charts, only in the fact that they are not fixed and visited from year to year. The manner of charting is the same in all (Clements 1905:167; 1907:206). The area desired, usually a meter or 10 meters, is staked out by means of quadrat tapes a centimeter wide and divided into centimeters, with eyelets at decimeter or meter intervals. The tapes are fixed by means of wire stakes, with loops at the upper end by which they are readily moved. The end tapes are placed to read from left to right, and the side tapes from top to bottom. After the quadrat is squared, the bottom tape is placed parallel to the top one, thus inclosing a strip a decimeter or meter wide for charting. This is charted decimeter by decimeter from left to right, and the upper tape is then moved to mark out the second strip for charting. The two cross-tapes are alternated in this fashion until the entire quadrat is plotted.

Special quadrat sheets are used for plotting (figs. 4, 5), which is always begun at the upper left-hand corner of the chart, the small squares aiding in determining the proper location of every plant. Each individual is indicated whenever possible, but mats, turfs, mosses, and thallus plants are outlined in mass as a rule. This is also done with large rosettes, bunches, and mats, even when they are single plants. Each plant is represented by the initial letters of the name. Signs may be used (Thornber, 1901:29), but they make charts difficult to grasp, and have the great handicap of differing for every investigator. The first letter of the generic name is used if no other genus found in the same quadrat or series of quadrats begins with the same letter. If two or more genera have the same initial, *e. g., Agropyrum, Allium,* and *Anemone,* the most abundant one is designated by *a,* and the others by the first two letters, as *al, an.* When a similarity in names would require three or more letters, *e. g., Androsace, Anemone,* and *Antennaria,* this is avoided by fixing upon an arbitrary abbreviation for one, viz, *at.* The number of stems from one base is often indicated by the use of an exponent, *e. g.,* a^3. Seedlings

are often distinguished by a line drawn horizontally through the letter, and plants in flower or fruit by a vertical line. In forest quadrats, seedlings are usually indicated by a small letter and mature individuals by a capital. In charting seasonal aspects, the rule is to indicate only the characteristic species, *i. e.*, those that flower at the time concerned.

The chief use of chart quadrats is for the comparison of different examples of the same community, or adjacent zones or stages of a sere. They are indispensable for the method of inference by which scattered stages are combined to show the course and sequence of a sere. Since permanent quadrats give all the values of simple chart quadrats, and many others besides, the chart quadrat should be used only when a single visit to a region makes the permanent quadrat unavailable.

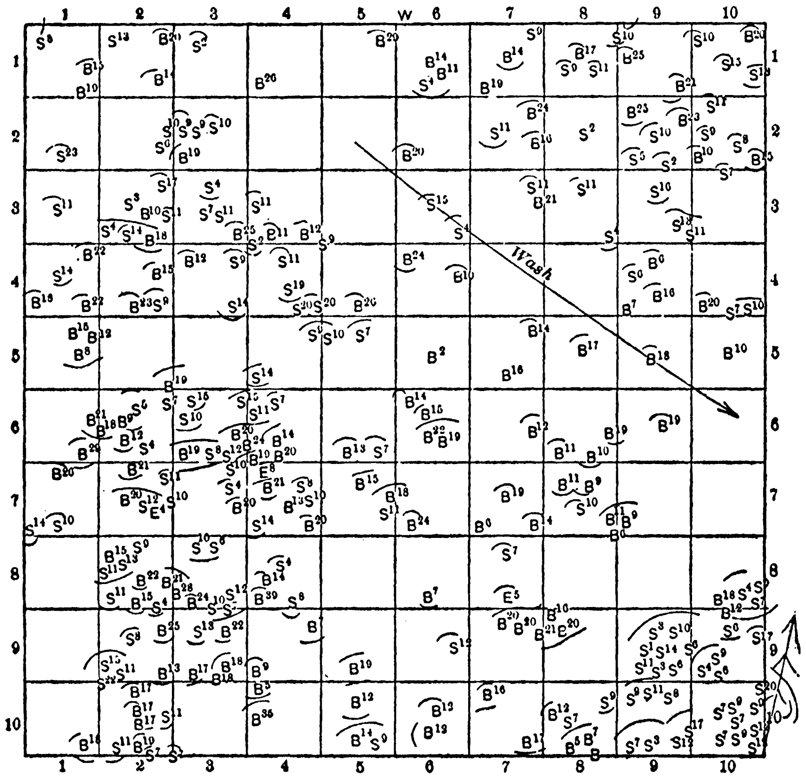


FIG. 4.—Quadrat showing reproduction in a complete burn, Long's Peak, Colorado.

Permanent quadrat.—In exact successional research it is imperative to be able to follow the course of development in detail from year to year, and especially from one minor sun-spot cycle to another. This is possible only by means of quadrats whose location and limits are fixed so that they can be relocated and charted from season to season, year to year, or from one period to another. These are termed permanent quadrats (Clements, 1905:170; 1907:208), since they make it possible to secure a complete record of all successional changes in the area studied. Naturally, they are always recorded

in the form of charts, though they may serve merely for an annual census of one or more species when this alone is desired. Permanent quadrats may be modified for various purposes, but they fall more or less completely into two groups, viz, permanent quadrats proper and denuded quadrats. The former are designed to reveal and record the changes shown by the different stages or associes of a sere; they make it possible to follow the course from one stage to the next. Denuded quadrats enable the student to reestablish earlier conditions in the area by removing the reaction in some degree, and to produce lacking stages at will. It is not only possible to reestablish every usual stage, but also to prepare a larger number of areas with minute reaction differences and thus obtain an analysis of associes possible in no other way. Most important of all exact methods is the combination of permanent and denuded

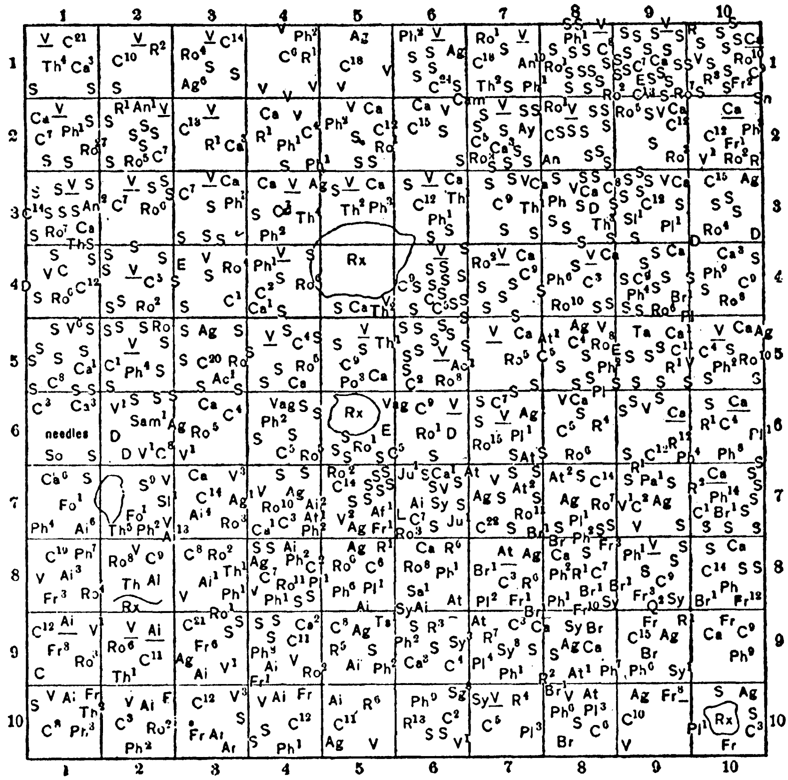


FIG. 5.—Quadrat showing seedlings of lodgepole pine in a *Vaccinium* cover, Long's Peak, Colorado.

quadrats into pairs, throughout a series of seral communities and zones, as is indicated later.

The permanent quadrat is staked out and charted in the manner already described for the chart quadrat. The selection of areas requires greater care, however, if they are to yield the best evidence of development. Like all accurate work, quadrating is slow, and hence the most important task is to secure the maximum results with the minimum number of quadrats. As a

rule, this means at least one quadrat in each consocies, with additional ones for important socies. As soon as the quadrat has been mapped and photographed, a labeled stake bearing the number and the date is driven at the upper left-hand corner, and a smaller one is placed at the opposite corner to facilitate the accurate setting of the tapes in later observations. It is also essential to select and record definite landmarks with care, in order that the location may be readily found again. In forest or scrub this is readily secured by blazing, but in grassland it is necessary to erect an artificial landmark, or to resort to compass and pacing.

At successive readings of a permanent quadrat, the tapes are placed in exact position by means of the stakes, and chart and photograph are made in the usual manner. To facilitate the study of the charts, four successive readings are recorded on the same sheet, thus greatly reducing the mechanical labor involved in comparing separate sheets. The same advantage is secured where the quadrat is used to show the variations from aspect to aspect of the same year. While the permanent quadrat reveals the actual changes in composition and structure which occur in the course of succession, a large part of its value is lost unless it is made a station for measuring the physical factors involved in ecesis, competition, and reaction.

Denuded quadrat.—A denuded quadrat (Clements, 1905:173; 1907:209) is a permanent quadrat from which the plant covering has been removed, after having been charted and photographed. Quadrats in bare areas, both primary and secondary, are essentially similar, but they differ in the impossibility of charting the original cover and of controlling the kind and degree of denudation. The denuded quadrat is especially adapted to the analytical study of ecesis and competition in relation to reaction. While denuding is an invaluable aid to the study of succession, it must be recognized that permanent quadrats register the exact course of development, while denuded ones make possible more definite analysis, and throw light upon stages not now available.

A quadrat which is to be denuded is first mapped, photographed, and labeled as for a permanent quadrat. The vegetation is then destroyed by removal, burning, flooding, or in some other manner. The kind and degree of denudation will be determined by the evidence sought. If it is to throw light upon an area in which denudation has affected the surface alone, the aërial parts may be removed by paring the surface with a spade, or by burning. To trace the effect of a more profound disturbance upon the reaction, the soil may be removed to varying depths, it may be dug up and the underground parts completely removed, or a sterile soil may be used to replace it. For obvious reasons, denuded quadrats are most valuable when used in connection with permanent quadrats, as indicated below.

Quadrat series and sequences.—In following the sequence of stages, the most valuable method is to use paired quadrats in each associes or consocies. Each pair consists of two permanent quadrats located side by side. After being mapped, one of them is denuded in the manner desired, and the two are then charted annually on the same sheet. If a battery of instruments for recording light, humidity, and temperature is located in the area, and the soil factors are determined for the two quadrats, a complete and accurate picture of succession is obtained. The permanent quadrats link the stages together as they occur; they fix the attention upon the process rather than upon the more

striking results. The denuded quadrats permit the ready analysis of the basic processes of migration, ecesis, competition and reaction, and the instruments furnish the necessary data as to the controlling physical factors.

If the analysis of processes and habitat is to be as thoroughgoing as possible, it is necessary to use a sequence of denuded quadrats. A time sequence is established by denuding one quadrat each year, each new area being separated by a space of a meter or so from the preceding one, so that invasion may occur from all sides. In this way it is possible to reproduce a complete series of stages, and to have them in close juxtaposition for comparative study. A quadrat sequence in space may also be used for the analysis of reaction, by denuding a series of areas in the same community in different ways or to different depths.

Various quadrats.—With more or less modification, the quadrat method may be applied to all plant communities, even in the most extreme areas. In fact, some of its most striking results are obtained with the pioneer communities in water and on rock. Chart quadrats of aquatic consocies are readily made, though permanent and denuded ones present obvious difficulties. Lichen and moss quadrats, on the other hand, are easily made permanent, or are readily denuded. Those under observation in the Rocky Mountains promise most interesting results, though the changes are necessarily slow. Subquadrats of parasitic and and saprophytic communities on bark, fallen trunks, and on the ground may likewise be made permanent, though the results are of secondary importance. Moreover, it seems probable that the use of soil quadrats will open a new field of study in enabling us to analyze the root relations of communities with much greater accuracy.

The transect.—The transect (Clements, 1905:176; 1907:210) is essentially an elongated quadrat. In its simplest form it is merely a line through a community or series of communities, on which are indicated the individuals of the species met with. The value of such a line transect lies chiefly in the fact that it reveals the larger changes of population, and hence serves as a ready means of delimiting ecotones. The belt transect consists of a belt of varying width, from a decimeter to several meters or more. It corresponds to the chart quadrat, and likewise gives rise to permanent and denuded transects.

A line transect may be made by pacing an area and noting the species and individuals encountered. The usual method is to run a transect by means of tapes. In the case of belt transects, two tapes are employed to mark out a strip of the width desired. In grassland and undergrowth, a transect 2 decimeters wide is most convenient, while in forest 1 or 2 meters wide is most satisfactory when reproduction is to be taken into account. When the adult trees alone are considered, the strip may be of any width. The transect is located in the area to be studied by running the tapes from one landmark to another, fastening them here and there by means of quadrat stakes. When it runs through a diversified area, particularly in the case of transects 100 to 1,000 m. long, the topography is determined by means of a transit, and the transect, when charted, is superimposed upon the topographic drawing. The charting of transects is done in the manner already indicated for quadrats. Because of their length, however, an assistant is almost indispensable in the work. To save the handling of many sheets, the practice is to record several

segments of a transect on the same sheet, when the width is not too great (fig. 6).

It is obvious that the belt transect, like the chart quadrat, is greatly enhanced in value if it is made permanent. The latter is readily done by means of careful blazing in woodland areas, but in grassland or in alternating woodland and grassland areas the use of a transit or at least of a compass is neces-

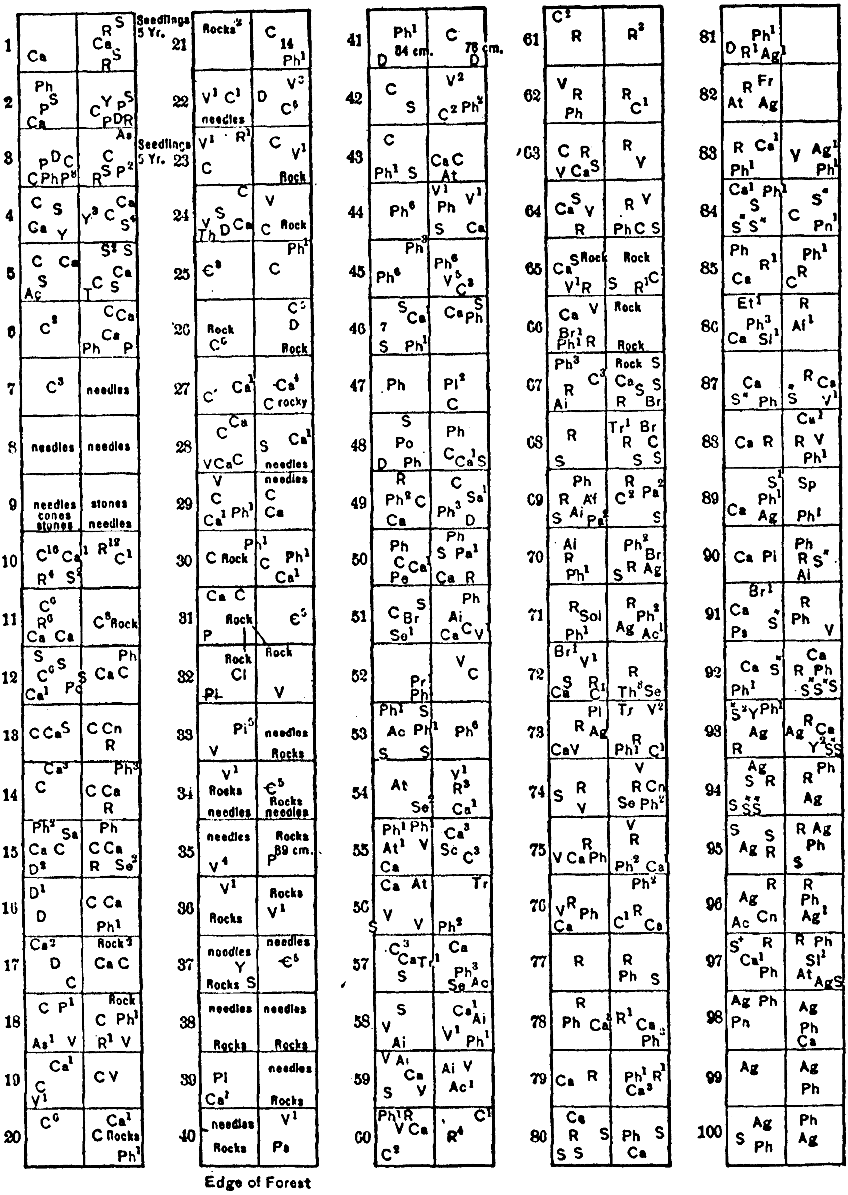


FIG. 6.—Belt transect through forest of lodgepole pine, bare burn and half burn, Long's Peak, Colorado.

sary. A label stake is driven at each end, on which is painted the number and date of the transect, as well as its direction and length. The position of the ecotones is indicated by smaller stakes bearing the transect number and the date when the ecotone was found at that point. These are left in place as they are added from year to year in order to indicate the shifting of the ecotone. This is the chief use of the transect, and serves well to illustrate the difference between the quadrat and transect. The permanent quadrat is intended to give the composition and structure of a typical or representative portion of a single community, and to enable one to follow its changes from year to year. A series of quadrats makes it possible to establish spatial comparisons between communities for any particular year, and has the incidental advantage of making it unnecessary to chart the intervening vegetation. This disadvantage of the transect, however, is more than offset by the unique values obtained by being able to trace the change in the typical structure and composition of a community or zone through the transition features of each ecotone into the adjacent zones. It has already been emphasized that zones are seral stages, and that ecotones make it possible to discover how one stage passes into another, *i. e.,* they are substages in essence. The transect alone makes it possible to follow in detail the change from one zone or associes to another through the ecotone, and hence is of the first importance in the investigation of succession, especially by the method of inference. In the case of grassland and forest undergrowth, a combination of quadrat and transect would seem to constitute the best method, but this has not yet been tried. If the quadrats of a series through several zones were connected by narrower transects, the maximum information would be obtained with the minimum expenditure of time and labor.

The denuded transect adds to the value of a permanent one by furnishing new stages for the analysis of each zone and ecotone; hence the two should be employed together wherever time and opportunity permit the most intensive study. The simplest method is to chart a permanent transect of twice the width, and then to denude one-half the width throughout. Since it is the colonization on the bare strip that is of importance, a permanent transect may be made in the usual way, and then a strip of equal width alongside of it denuded without being charted.

The bisect.—The layer transect (Clements, 1905:180) is used to show the vertical relations of species in a layered community. Its value in succession lies chiefly in recording the successive disappearance of layers as the climax is reached. It has further value in tracing the beginnings of layering as competition passes into the dominance of medial stages. In all of these cases, root relations play an important and often a controlling part. Hence they constitute an essential portion of the record, and it is proposed to indicate the vertical and lateral relations of individuals by means of a cross-section showing both shoots and roots in their normal position. Such a cross-section may be termed a *bisect* (figs. 7, 8). In a purely diagrammatic form it has frequently been used to show the relations of aquatic and swamp plants, but as a means of showing the exact relations of layers, especially in the soil, it was first employed by Yapp (1909:288) and Shantz (1911:51). The latter used it primarily to illustrate the reaction of root-layers upon water penetration, and the consequent effect upon the course of succession. There is no question

that investigations of this sort must become increasingly frequent in the study of development, and that the bisect will become a regular method of investigation and record (*cf.* Weaver, 1915, 1916).

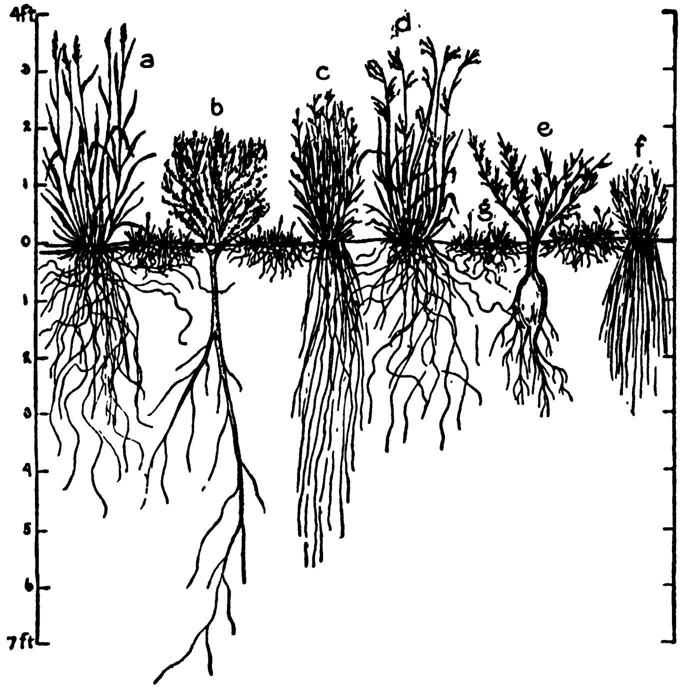


FIG. 7.—Bisect of sandhills mixed association in eastern Colorado. *a, Calamovilfa longifolia; b, Artemisia filifolia; c, Andropogon scoparius; d, A. hallii; e, Ipomoea leptophylla; f, Aristida purpurea; g. Bouteloua hirsuta.* After Shantz.

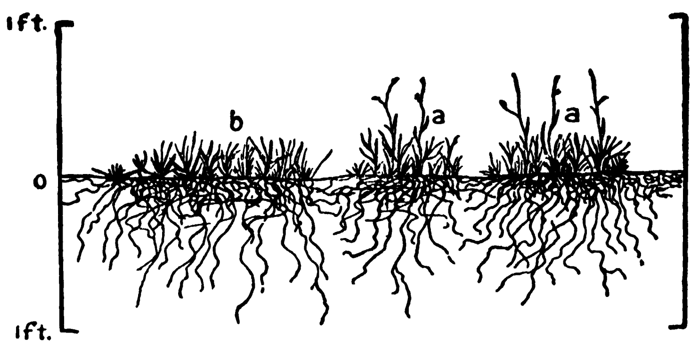


FIG. 8.—Bisect of the *Bulbilis-Bouteloua-poion* in eastern Colorado. *a, Bouteloua gracilis; b, Bulbilis dactyloides.* After Shantz.

The migration circle.—The migration circle (Clements, 1905 :182 ; 1907 :212), or *migrarc*, is designed to make possible the exact analysis of migration, especially without reference to ecesis. Practically all studies of migration have

been based upon the establishment of individuals, and there has been almost no attempt to determine the rôle of migration itself in succession, as one of the two processes concerned in invasion. A few studies have been made of the kind and number of migrules brought by long-distance carriage, such as that of birds, but these have little or no effect upon succession. Local, and usually mass, migration is the chief factor in the latter, and such movement permits of fairly accurate measurement, even though ecesis is not taken into account.

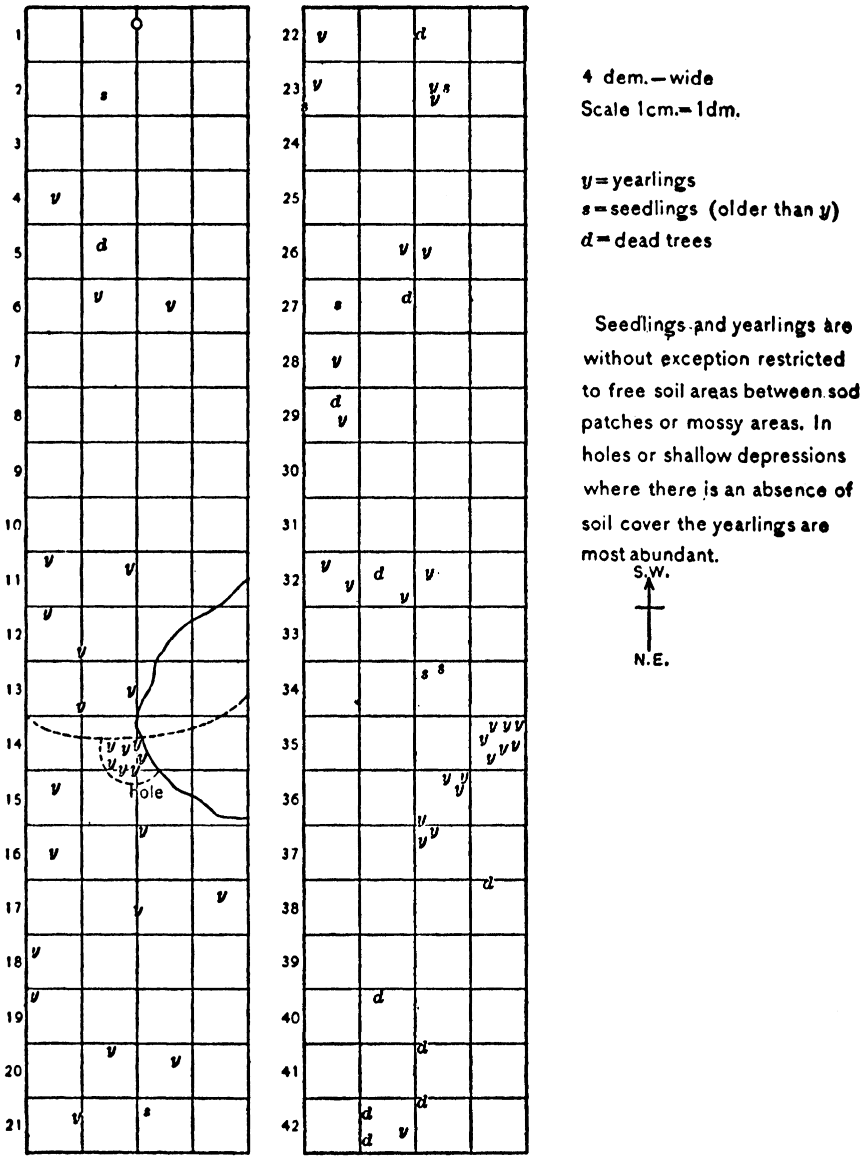


FIG. 9.—Transect of a migration arc, Uncompahgre Plateau, Colorado.

A migration circle or arc may be located with reference to an individual, a community or a distinct ecotone, such as the edge of a forest. In the case of an individual, or a small family or colony, a circle, or better, a series of concentric circles, is marked out. This may be done by carrying a radius around the object, or, better still, where the study is to take some time, by means of concentric circles made by using a tennis-court marker. When the migration is in a single general direction, as at a forest edge, concentric arcs or parallel lines are used, as the size of the community demands. The determination of migration alone demands the most minute study, and hence it is difficult to carry it throughout a season. In the case of wind-borne germules, it can best be determined after times of high wind, or, still better, at times of varying velocities which are measured. The detection of seeds and fruits in vegetation is so time-consuming, even when it is possible, that the study of actual movement can best be made upon snow surfaces or upon the bare ground. In the case of individual plants, especially trees, a denuded area in the direction of usual movement is the most satisfactory. When the study of migration receives the detailed attention which its importance warrants, it is probable that quadrats artificially prepared to catch and retain the migrules brought to them will be placed at definite intervals in the direction of migration. At present, the measurement of effective migration in terms of ecesis furnishes the most convenient method. This has been used with signal success in investigating the invasion of "natural parks" by *Picea* and *Abies* in the Uncompahgre Plateau of Colorado (fig. 9) and recently by Hofmann (1916) in studying secondary succession in the Pacific coniferous climax.

METHODS OF MAPPING.

Methods.—Schröter (1910:127) has discussed at length the methods of ecological cartography. Such macrographic methods are not considered here, as they have little or no bearing on the intensive study of succession. This is due to the fact that succession has usually not been taken into account at all, though it is obvious that the areas mapped may be readily distinguished as climax and developmental. The methods indicated below are micrographic in the sense of Nilsson in that they deal with individual plants or communities. They may be distinguished as (1) extensions of the quadrat method, (2) ecotone and community mapping, and (3) combined quadrat and map method. The first is illustrated by the method of squares and the gridiron method of Oliver and Tansley (1904:228, Tansley 1904:200). The gridiron method appears to be very similar to the use of perquadrats of 25 feet, but differs in that the contours and the outlines of communities are indicated rather than the individuals. The method of squares employs areas 100 feet square, which are used to cover continuously the entire area to be mapped. Physical features, contours, and the boundaries of communities are alone shown, though the gridiron method may be used to furnish greater detail in various areas.

Community charts and ecotone maps.—Community charts (Thornber, 1901:126) resemble closely the gridiron maps of Oliver and Tansley. They are made by means of pacing or by tapes. They may be employed to map in some detail the dense vegetation of an associes or association, but their greatest value lies in indicating the position and growth of families and colonies in

bare areas. Community charts combine quadrat and map methods, in that they deal chiefly with the outline of units, but they are on such a scale as to show much of the detail as to composition.

Ecotone maps (Clements, 1905:181) have to do with the relations of zones and alternes. Because of the essential relation of the latter to succession, such maps furnish a graphic summary of the course of development, either actual or potential. In the one case, the map shows the zones or stages of an actual sere on a small scale, as in the case of ponds and streams. In the other, the zoned climax associations of an entire region are shown on a large scale in the potential sequence of the clisere. In either case, the map is constructed by locating and tracing the ecotones between the various zones, usually with the topographic features indicated in so far as they have a bearing upon development.

Survey maps.—In the methods of vegetation survey developed by the Botanical Survey of Minnesota, an endeavor has been made to combine the advantages of topographic and ecotone maps with those of quadrats. From the nature of American subdivisions, the unit is the township, consisting of 36 square miles or sections. Each section is divided into four quarter sections a half mile square, and each of these into "forties" a fourth of a mile square. The mapping unit is the "forty." This is mapped on a square decimeter of cross-section paper, the four maps for each quarter section being placed in their proper relation upon one sheet. The scale is approximately 1 to 4,000. Topographic and artificial features and the ecotones of communities are mapped in detail. Cultural as well as natural communities are indicated, while at least one quadrat or transect is charted for each "forty," the number depending upon the differentiation of the vegetation in it. Instrument readings are taken in the quadrats or at the ecotones, and photographs are made to accompany the charts throughout. As a consequence, a complete record is obtained of topography and the structure and development of vegetation, with some idea of the physical factors involved as well. When supplemented by intensive studies of prisere and subsere in the different climaxes, a complete picture of the vegetation is obtained. The application of the results of such a survey also becomes a matter of prime importance to forestry and grazing and to the agriculture of new or neglected regions.

Climax maps.—The general treatment of vegetation as static has resulted in the production of many maps in which no distinction is drawn between climax and developmental communities. From the nature and extent of climax formations, vegetation maps of regions and continents have been concerned with them primarily, but with little or no recognition of basic developmental relations, such as that of the clisere. Vegetation maps have been constructed from many sources of diverse value, and can only be regarded as provisional to a large degree. The existence of a great climax vegetation is so patent that its general area can readily be indicated, but its definite relation to other climaxes, its exact boundaries, and especially the problems of such transition areas as prairie, chaparral, and mixed forest can only be settled by intensive studies. Hence the construction of reliable climax maps must follow the investigation of developmental relations and the accurate tracing of great ecotones rather than precede them, as has usually been the case. However, it is clear that it is necessary to construct such maps from time to time as our

knowledge grows, in order that they may serve as working bases for further refinement. For the present the methods of cartography already in use for macrographic maps will suffice, but it seems clear that these must be largely worked over when maps come to be used to show primary developmental relations.

INSTRUMENTAL METHODS.

General considerations.—While there has been a notable advance in the use of instruments since the appearance of "Research Methods in Ecology" (1905), the instrumental study of vegetation is still far from the rule. This is strikingly true of succession, for the additional reason that developmental studies themselves are still exceptional. As indicated in the discussion of reactions, the use of instruments in studying successional processes was begun in America more than a decade ago, but it is only during the last two or three years that instrumentation has become a general procedure in this country and in England. Elsewhere, even in Scandinavia, where developmental studies have long been the rule, the instrumental study of successional processes is still infrequent. There are evidences, however, that this condition is disappearing, and we can look forward confidently to a time when succession will become the basic method of vegetation research, and when it will use instrument and quadrat as its most indispensable tools.

The chief use of instruments so far has been in attempting a complete or partial analysis of the habitat. All careful work of this sort furnishes data for succession, but much of it is difficult of application or interpretation. As a consequence, the use of instruments in developmental study must be directed to the critical processes in succession. These are reaction, ecesis, and competition. The first of these is clearly the most important, because of its control of the movement of successive populations, but its effect in plant terms is measured by ecesis and competition also. The critical effect of reaction is felt at the time of germination, and when competition between the mixed populations of a mictium is passing into the dominance of the next stage. Hence the measurement of reaction has its greatest value when it is directed to these two points. It must also be recognized that reaction is itself a complex process, in which all of the factors of the habitat may be concerned. Here, again, it is essential to keep in the main path, and to concentrate upon the primary reactions which direct the actual sequence of stages. As has been shown in Chapter V, the primary reactions are upon water and light, and upon the stability of the soil, though the latter can perhaps best be measured in terms of humus and water-content. In some cases, reaction upon nutrient content plays a primary rôle, as perhaps also that upon water by which it becomes acid. It is clear that these two reactions may also be intimately bound up with each other. In initial and medial stages the edaphic reactions are controlling, but in the final stages of scrub and forest formations the light reaction is decisive. At the same time the water reaction can not be ignored, as Fricke has demonstrated (p. 93). The local climatic reactions of forests may ultimately prove of much importance, but they would seem to play only a subordinate part in the development of a particular sere.

The instrumental study of succession must be made chiefly in the *reaction-level.* This is the level which is bisected by the surface and is characterized

by the maximum effect of reaction. It is the level also in which the critical decisions as to ecesis and competition are reached. The measurement of reaction at other levels is not without value, but it is rarely of primary importance. Since the critical period for each species is usually the seedling stage, it indicates that the depth of the reaction-level above and below the surface is only a few inches, or at most a foot or so. This greatly narrows the field of measurement, and makes the application of the results much easier. The most critical area of all is where the reaction-level of one community meets that of another, *i. e.*, the ecotone. This is strikingly illustrated by the reciprocal behavior of the seedlings of both communities at the ecotone between grassland and forest. It is in such areas that reactions can be best determined and their influence measured.

Measurement of reactions.—The methods of instrumental investigation (Clements, 1905:20; 1907:7, 73) are now so numerous and detailed that no adequate account of them can be attempted here. It must suffice to point out the general method of attack and to emphasize the necessity of such study for the understanding of succession. At the outset, it must be recognized that general measurements, such as are made in the usual meteorological observations, are of little or no value. This is true to some extent also of the data obtained by ecograph batteries in various habitats. These bear some relation to the conditions in actual control of ecesis and competition, but the direct attack must be made upon these conditions themselves, since they characterize the reaction-level. Thus, while the experienced investigator may find it possible to interpret and apply general factor data, one can expect to obtain little light upon succession unless the instrumental study is concentrated upon the factors in primary control. This means that water and light reactions must be given the first place, though it is certain that water reactions in particular must ultimately be carried further back into the plexus of intricate cause-and-effect relations found in the soil. Moreover, in dealing with water and light, it must be borne in mind that the reaction may affect the quality as well as the quantity, and that humidity as well as water-content must be considered. Finally, it should be recognized that, while instruments furnish the readiest means of measurement, the use of standard plants for determining the effect of each reaction brings us much nearer to the explanation sought.

Measurement of water reactions.—The reaction of a community upon water may affect the amount of holard and echard, or the degree of humidity. It may change the nature of the water-content by modifying the nutrient content, by making it acid or decreasing its acidity, or by decreasing its alkalinity. So far as is known the alkalinity of the soil can not be increased by the accumulation of plant remains in it, except by artificial means. The development of instruments and instrumental methods for the study of water-content and humidity has gone so far that even a brief mention of them is impossible in the scope of the present discussion. The great majority of them have not been developed with reference to succession, and hence the number which require mention is small. Those of the first importance for the accurate field study of reaction are: (1) determination of the holard in the reaction-level of the soil, and especially at the germination level; (2) determination of chresard and echard at the depth of various roots in the reaction-level, since the

addition of humus, and often the abstraction of water also, decreases from the surface downward; (3) measurement of humidity and evaporation in the chief reaction level of the air, and especially at the soil-surface, where the effect upon the seedling is critical; (4) determination of the degree of acidity of soil-water at different depths; (5) determination of the degree of alkalinity at different depths.

Methods of determining the holard are so numerous and so simple as to need little comment. From the standpoint of succession, however, it is imperative to determine the holard at levels marked by the root-layers, and especially in the soil-layer occupied by the roots of dominants. But, while it is an easy matter to measure the reaction in terms of increased water-content, the successional significance of this increase can be determined only by ascertaining the amount of it available, *i. e.*, the chresard. Our knowledge of this available water and of the water requirements of plants has greatly increased since the chresard was emphasized as the critical factor in vegetation (Clements, 1905:30; 1907:9). In spite of the excellence of the work done under control conditions (Briggs and Shantz, 1912; Crump, 1913:96; 1913²:125), it seems certain that the rôle of the chresard in succession can only be determined under field conditions, owing to its variation at different soil-levels and perhaps with the conditions for transpiration. The measurement of evaporation has been so standardized by the porous-cup method in the work of Livingston (1910:111) and others, and by the open water method of Briggs and Belz (1910:17) that there is little left to be desired. Readings of humidity, temperature, and wind have become unnecessary, except as they are required for the analysis of evaporation or for other purposes. In the case of evaporation, however, while this gives a measure of reaction, it may not have a causal connection with succession. This is apparently the case in the successive consocies of scrub and forest, where the evaporation decreases toward the climax, but the reaction in control of the sequence is that upon light. Moreover, evaporation measures fail to reckon with the compensating effect of water-content, and it seems inevitable that measures of transpiration be largely substituted for those of evaporation in the study of seral reactions. Considerable success has already been attained in selecting species and standardizing individuals for this purpose, and the method gives promise of universal application. Until we have a clearer notion of the actual effect of an acid holard, the present methods of determining the degree of acidity by means of litmus or phenolphthalein are fairly satisfactory. It seems increasingly certain, however, that the acid is merely a by-product of decomposition under a lack of oxygen, and that the absence of oxygen is the real factor. Experiments now under way seem to prove this, and hence to indicate that measurement of the primary reaction in acid soils must be directed toward the effect upon the oxygen content, *i. e.*, upon aëration. The determination of the alkalinity of the soil solution has been so thoroughly worked out by Briggs (1899) by means of electric resistance apparatus that it seems to leave nothing more to be desired.

Measurement of light reactions.—Since the pioneer work of Wiesner (1895) in measuring light intensity, a number of methods have been devised to measure light values (Clements, 1905:48; 1907:72; Zon and Graves, 1911). Most of these have had to do with light intensity, but the spectro-photometers of Zederbauer (1907) and Knuchel (1914) have been devised for the purpose

of determining the quality of forest light. Most instruments for measuring light intensity have been based upon the use of photographic paper. Theorectically this is unsatisfactory, because only the blue-violet part of the ray is measured. Practically, however, the use of such photometers for more than 15 years has furnished convincing evidence that it is a very satisfactory method of measuring the effect of light in the structure and development of communities and the adaptation of species. In the endeavor to organize the whole field of light instrumentation, the writer has designed and used with steadily increasing efficiency the following series of photometers: (1) simple photometer; (2) stop-watch photometer; (3) water photometer; (4) selagraph, or recording photometer; (5) spectro-photometer. The construction and operation of these are described in detail in a forthcoming paper. In addition, a further effort is being made to develop a method by which standardized plants are employed for determining the amount of photosynthate in different seral stages.

GROWTH METHODS.

Ring-counts.—In determining the successional relations, and especially the sequence of woody dominants and subdominants, determinations of the respective ages by counts of the annual rings is of the first importance. This is especially true of supposed cases of degeneration of forest or its conversion into scrub, heath, or grassland. There is no substitute for this method, except the all but impossible one of tracing the course of development throughout, which would require more than a life-time. It is for this reason that all reported cases of natural degeneration or conversion have been called in question, as well as many of those where the operation of artificial factors is slow. In none of these have the exact methods of ring-counts and quadrats been employed, and in consequence the conclusions reached can only be regarded as working hypotheses. In the more minute studies of sequences and of dates it has been found possible to determine the ages of perennial herbs, by the rings as well as by the joints of their rhizomes or other underground parts. This is of particular value in the study of colonization after fire or other denuding forces. Ring-counts can be used to the greatest advantage in ascertaining the relations of dominants in mictia and in ecotones, but they are also indispensable in determining the seral significance of relicts. In fact, the recognition of relicts often depends wholly upon the determination of respective ages. In reproduction, especially under competition, and particularly where forest or scrub is in contact with grassland, the ages of the invading trees or shrubs at various distances from their community is indispensable to a knowledge of the present success and the future outcome of the invasion.

A detailed account of methods of counting rings seems unnecessary because of the general simplicity of the problem. Certain precautions are necessary, however, as well as great care in the actual process of counting the rings (Clements, 1907, 1910; Douglass, 1909, 1913, 1914; Huntington, 1914). Stump-counts are desirable as a rule, but in many cases the increment borers of foresters can be used to advantage. Fortunately, lumbering and clearing usually furnish the necessary stumps, though the intensive study of succession over many areas can only be carried on by the constant use of ax and saw.

Burn-scars.—The method of using ring-counts and the scars left by fire upon trees and shrubs for determining successional changes, as well as the dates of their occurrence, is described in the following extract (Clements, 1910:9).

"The basic method of reconstructing a burn has been to determine the ages of the oldest plants which have come in since the fire, applied both to the trees and to the shrubs and perennial herbs of each type. It takes account of dead trees and shrubs, standing and fallen, in addition to the living ones. The method of fire-scars is of equal importance, though often less available. Where the same area has been burned over two or more times this method is of unique value, for it is not unusual to find double and even triple scars. The nature, position, and extent of fire scars are of equal importance. Any evidence left by a fire upon a woody plant is regarded as a scar. Hence it is possible to distinguish top scars, trunk scars, and base scars with respect to position, and bark scars and wood scars with respect to depth. Heal scars and hidden scars occur on living trees, while white scars and cinder scars are found on dead or drying trees. In addition to ages and scars, the observation of soil layers is often of great help. The presence or absence of a cinder layer or of cinder pockets, or of an organic layer or cover often goes far to check or confirm the evidence drawn from ages or scars.

"The evidence of age drawn from annual rings is usually so clear and decisive as to be beyond question. Occasionally with seedlings, and often in the case of suppressed trees, it is impossible to make an absolute count of rings, even by means of microscopical sections. In practically all such cases an examination of other individuals is conclusive.

"A distinction between fire-scars and scars due to other causes is sometimes made with the greatest difficulty, and in rare cases is altogether impossible. In most cases, however, it is possible to recognize a fire scar with certainty. In actual practice the method was to require evidence of charring wherever the age of the scar did not check with that of neighboring scars. Chance scarring by lightning or by a camp fire, often in unexpected places, is of sufficient frequence to explain the departure of any charred scar from the normal. The position of a scar often serves to determine whether it belongs to a particular fire or is a mere chance scar. Heal scars abound at the edges of a burn, and consequently those caused by the same fire occur on the same side, namely, that from which the fire came. Occasional exceptions arise where a ground fire has unexpectedly worked to the surface, but these are nearly always determined by a careful scrutiny. The nature of fires and their severity is indicated, as a rule, by the depth of scars, and the predominance of bark scars or wood scars is used to determine the relative order of two or more successive fires. Scars from successive fires are often united in double or triple scars on either dead or living trees, and these give the best of all evidence upon the succession of fires and the burn forests which follow them. In using the depth or nature of scars as a guide the fact was considered that forests regularly contain dead standing trees, some of which may have lost their bark. It is evident that the same fire would cause at least three different kinds of scars in such stands; that is, heal scars, usually basal, on the surviving trees; bark scars on the living trees killed by the fire; and wood scars on the dead trees. The wood scars would, moreover, be cinder scars wherever the bark had fallen off before the fire had occurred.

"Finally, the data obtained from fire scars were checked by a count of the annual rings formed since the scar was made. The most careful use of the evidence from fire scars and from annual rings can not eliminate the possibil-

ity of an error of one year in determining the date of a fire. This is because the time of the growing season at which a fire occurs determines whether growth or germination may begin that year. With scars and root suckers on trees which remain alive, it is probable that growth begins the year of the fire, unless it occurred in the fall or early winter. On the other hand, it is equally probable that seeds remain dormant until the following year, unless the fire occurs in spring or early summer. The majority of fires occur after midsummer. If the growing season is not over, scars and root suckers will show one more ring than the pines and perennial herbs which appear the next year. If it is after growth ceases, scars, root sprouts, pine seedlings, and perennials will agree in the number of rings. In most of the burns studied, scars formed the first ring the year of the fire, while the pine seed did not germinate until the next spring. In the burn of 1905 the aspen-root sprouts followed the fire immediately, but in the burns of 1901 and 1878 aspens and pines appeared together the year after the fire. Therefore the following simple rule was used to determine the year of a fire: Subtract the number of rings of a scar, or the number of rings plus one of a seedling or tree, from the year in which the count is made. This rule assumes that the trunk is cut sufficiently low to show the first year's growth. With lodgepole it was necessary to cut the trunk at the surface of the ground, or on slopes, below the surface."

PLANT INDICATORS

THE RELATION OF PLANT COMMUNITIES TO PROCESS AND PRACTICE

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XI. CONCEPT AND HISTORY.

The practical aspect.—Every plant is a measure of the conditions under which it grows. To this extent it is an index of soil and climate, and consequently an indicator of the behavior of other plants and of animals in the same spot. A vague recognition of the relation between plants and soil must have marked the very beginnings of agriculture. In a general way it has played its part in the colonization of new countries and the spread of cultivation into new areas, but the use of indicator plants in actual practice has remained slight. It is obviously of greatest importance in newly settled regions. However, it is in just these regions that experience is lacking and correlation correspondingly difficult. In fact the pioneer is often misled by his endeavor to transfer the experience gained in his former home to a new and different region. Differences of vegetation and climate, and often of soil as well, make a wholly new complex of relations. As a consequence, the settler is very apt to go astray in reaching conclusions as to the significance of a particular plant. As the country becomes more settled, experience accumulates and makes it increasingly possible to recognize helpful correlations. But this period usually passes too quickly to establish a procedure before the native plants have disappeared, except from roadsides, meadows, and pastures. The manner and degree of utilization of natural meadows and pastures are clearly indicated by the plants in them. Yet it is exceptional that these indicators are recognized and made use of by the farmer.

The scientific aspect.—On the scientific side, the concept of indicators could hardly be expected to emerge until plant physiology had made a beginning. Looking backward, one discerns something of this idea in the studies of vegetational changes by King (1685:950), Degner (1729), Buffon (1742:234, 237), and Biberg (1749:6, 27). It is likewise suggested in the description of stations by Linné (1751:265) and especially by Hedenberg (1754:73). The basic correlations were made definite by De Luc (1806: Plant Succession, 10) in his studies of succession in peat-bogs and by Schouw (1823:157, 166) in the classification of plants by habitats. The idea is more or less in evidence in the long series of observations and discussions relating to the chemical theory of the influence of soils. The chief proponents of the chemical theory were Unger (1836), Sendtner (1854), Naegeli (1865), Fliche and Grandeau (1873), Bonnier (1879), Contejean (1881), Hilgard (1888, 1906), and Schimper (1898, 1903). The founder of the physical theory was Thurmann (1849), though his views necessarily placed his results in more or less harmony with the water-content classification of Schouw. The century-old controversy over the chemical theory has centered around the question of the importance of lime in the soil. Though the broadening of ecological research has thrown this question more and more into the background, there is still anything but unanimity of opinion concerning it. While it is felt that the problem can be solved only by more comprehensive and thoroughgoing experimentation than it has yet received, the several divergent views are later considered briefly for the sake of a clearer appreciation of existing opinion. Finally, the many

studies of foresters upon the tolerance of trees to shade had large elements of indicator value, but these were never brought together into a system.

Studies of the relation of plants to soil were based upon the response of the individual or species. The first serious attempt to organize these into a system of indicator plants was made by Hilgard (1860, 1906). In a similarly virgin region, Bessey (1891, 1901) also recognized the indicator value of native plants, and especially vegetation, for the proper development of agriculture. His ideas of the practical value of vegetational studies stimulated the development of ecology as recorded in the "Phytogeography of Nebraska" (Pound and Clements, 1898, 1900) and the "Development and Structure of Vegetation" (Clements 1904:1). In the latter the need of quantitative studies of habitat and community and the importance of succession were first emphasized, and these were made the basis of a definite quantitative system in "Research Methods in Ecology" (Clements, 1905). As a consequence, the way was prepared for the use by Shantz (1911) of the plant community as an indicator with particular reference to succession. In another direction, E. S. Clements (1905) made a searching investigation of the relation of leaf structure to different factors and habitats and laid the foundation for the use of habitat-forms and ecads as indicators.

The development of the idea that plants are indicators of climate is more difficult to trace. Tournefort (1717) probably furnished the first recorded instance of the idea, when he pointed out that the slopes of Mount Ararat showed many species of southern Europe, while still higher appeared a flora similar to that of Sweden, and on the summit grew arctic plants such as those of Lapland. Perhaps the most important studies of climatic zones of vegetation were those of Humboldt and Bonpland (1805:37), Kabsch (1855:303), Köppen (1884:215), Drude (1887:3), and Schimper (1898, 1903:209). In none of these is there a distinct recognition of the indicator concept. This is likewise true of the formulation of life zones and crop zones on the North American continent by Merriam (1898). His applications of the indicator idea are so numerous and definite, however, that he must be given the credit for organizing the first system of climatic indicators. As to the soil, Hilgard is to be regarded as the pioneer in recognizing the great possibilities of systems of indicators and applying this on an adequate scale, and Shantz as the investigator who has placed the whole matter upon an adequate scientific basis.

HISTORICAL.

In a general account of the important steps in the spread of the indicator concept, it appears best to deal only with those studies in which the concept is either evident or actually stated. There are numerous books and papers on plant-geography, forestry, and agriculture, which have some general relation to the idea. Most of these have contributed nothing tangible or important and for the most part are ignored. A few are considered or mentioned in the proper special sections. Entire justice might demand consideration of the work of Bonnier, Fliche and Grandeau, and Contejean at this point, but for many reasons it has proved undesirable to treat these in detail. The following accounts are of those researches in which the term indicator is

actually employed or in which the use of instrument, quadrat, or successional methods gives them distinct indicator objectives.

AGRICULTURAL INDICATORS.

Hilgard, 1860.—The following excerpt will serve to show that Hilgard was the first investigator to recognize clearly the importance of indicators in soil studies and to make actual use of them in determining the agricultural possibilities of new lands. A further account of his views and results is given on a later page.

"Judging of land by its natural vegetation. The distinction just mentioned, so far from being of merely theoretical value, is one of the highest practical importance. Agriculturists are accustomed to judge of the quality of lands by the natural vegetation which they find upon it; and they rarely direct their attention to anything but the forest trees. Yet these are, for the most part, indicative rather of what, in the *agricultural* sense is termed the *subsoil,* than that of the surface stratum usually turned by the plow, in the shallow tillage prevailing at present, which may be of a totally different character.

"As a general thing, the forest growth when considered not only with regard to the *kind* (species), but also to the *form* and *size* of the trees, is a very safe guide in judging of the quality of land, and the systematic study of the subject in connection with analyses of soils, promises results of a highly practical importance, which it is intended to communicate more fully in a future report. But this criterion may not infrequently lead to grave mistakes unless a proper examination of the soil and subsoil be made at the same time.

"These examples may suffice to show that while in the forest trees we possess trustworthy guides to a knowledge of the character of the material in which their roots are buried, it is quite essential to determine at the same time, by inspection, that it is the arable soil itself, and not merely the subsoil, which is thus characterized; and we should especially make sure that the smaller plants, viz., the shrubs and perennials, corroborate the evidence of the trees. Annuals are less reliable in their indications because their development is to a greater extent influenced by the accidental circumstances of the seasons."

Chamberlin, 1877.—Chamberlin shares with Hilgard the honor of being a pioneer in the use of native plants to indicate the agricultural possibilities of a region (1877:176). He deserves especial credit for being the first to recognize that the community was a better indicator than the species, and for classifying the vegetation of Wisconsin into communities with more or less definite indicator value. Several of Chamberlin's associates on the Geological Survey of Wisconsin made more or less use of his system of indicators (Wooster, 1882:146; King, 1882:614; Irving, 1880:89), though it unfortunately appears to have remained unknown to botanists, and consequently led to no further work in this field.

"The most reliable natural indications of the agricultural capabilities of a district are to be found in its native vegetation. The natural flora may be regarded as the result of nature's experiments in crop raising through the thousands of years that have elapsed since the region became covered with vegetation. If we set aside the inherent nature of the several plants, the native vegetation may be regarded as a natural correlation of the combined agricultural influences of soil, climate, topography, drainage and underlying formations and their effect upon it. To determine the exact character of each

of these agencies independently is a work of no little difficulty; and then to compare and combine their respective influences upon vegetation presents very great additional difficulty. But the experiments of nature furnish us in the native flora a practical correlation of them. The native vegetation therefore merits careful consideration, none the less so because it is rapidly disappearing, and a record of it will be valuable historically.

"It is rare in nature that a single plant occupies exclusively any considerable territory, and in this respect there is an important difference between nature's methods and those of man. The former raises mixed crops, the latter chiefly simple ones. But in nature, the mingling of plants is not miscellaneous or fortuitous. They are not indiscriminately intermixed with each other without regard to their fitness to be companions, but occur in groups or communities, the members of which are adapted to each other and their common surroundings. It becomes then a question of much interest and of high practical importance to ascertain, within the region under consideration, what are the *natural groupings* of plants, and then what areas are occupied by the several groups, after which a comparison with the soils, geological formations, surface configuration, drainage and climatic influences, can not fail to be productive of valuable results.

"The following natural groups are usually well marked, though of course they merge into each other where there is a gradual transition from the conditions favorable for one group to those advantageous to another. In some instances it is unquestionably true that other circumstances than natural adaptability control the association of these plants, and an effort has been made in the study of the region, to discern these cases and eliminate them from the results, so that the groups that are given here are believed to be natural associations of plants. Their distribution is held to show in what localities conditions peculiarly advantageous to them occur, and hence advantageous to those cultivated plants that require similar conditions."

The author has used both class and group as synonyms of community, but the latter term is substituted in the following list for the sake of clearness:

A. Upland vegetation.
   (1) Herbaceous.
   1. Prairie community.
   (2) Arboreous.
   2. Oak community.
   3. Oak and maple community.
   4. Maple community.
   5. Maple and beech community.
   6. Hardwood and conifer community.
   7. Pine community.
   8. Limestone ledge community.
   9. Comprehensive community.

B. Marsh vegetation.
   10. Grass and sedge community.
   11. Heath community.
   12. Tamarac community.
   13. Arbor vitae community.
   14. Spruce community.

C. Communities intermediate between upland and marsh.
   15. Black ash community.
   16. Yellow birch community.

Merriam, 1898.—In "Life Zones and Crop Zones," Merriam summarized the experiential evidence as to the climatic indications for crop plants. This was arranged in relation to seven life zones based theoretically upon temperature, but determined for the most part by the distribution of native plants and animals. As a pioneer attempt to organize a vast field, it deserves great credit, even though later studies have rendered his zonal classification of secondary value. The author's understanding of the nature and scope of climatic indicators is best shown by the following excerpts:

"For ten years the Biological Survey has had small parties in the field traversing the public domain for the purpose of studying the geographic distribution of our native land animals and plants, and mapping the boun-

daries of the areas they inhabit. The present report is intended to explain the relations of this work to practical agriculture and to show the results thus far attained.

"It was early learned that North America is divisible into seven transcontinental belts or *life zones* and a much larger number of minor areas or *faunas,* each characterized by particular associations of animals and plants. It was then suspected that these same zones and areas, up to the northern limit of profitable agriculture, are adapted to the needs of particular kinds or varieties of cultivated crops, and this has since been fully established. When, therefore, the natural life zones and areas, seemingly of interest only to the naturalist, were found to be natural crop belts and areas, they became at once of the highest importance to the agriculturist. A map showing their position and boundaries accompanies this report, and lists of the more important crops of each belt and its principal subdivisions are here for the first time published. The matter relating to the native animals and plants has been reduced to a fragmentary outline for the reason that this branch of the subject is of comparatively little interest to the farmer and fruit-grower." (p. 7.)

"The Biological Survey aims to define and map the natural agricultural belts of the United States, to ascertain what products of the soil can and what can not be grown successfully in each, to guide the farmer in the intelligent introduction of foreign crops, and to point out his friends and enemies among the native birds and mammals, thereby helping him to utilize the beneficial and ward off the harmful kinds." (p. 9.)

"The farmers of the United States spend vast sums of money each year in trying to find out whether a particular fruit, vegetable, or cereal will or will not thrive in localities where it has not been tested. Most of these experiments result in disappointment and pecuniary loss. It makes little difference whether the crop experimented with comes from the remotest parts of the earth or from a neighboring State, the result is essentially the same, for the main cost is the labor of cultivation and the use of the land. If the crop happens to be one that requires a period of years for the test, the loss from its failure is proportionately great.

"The cause of failure in the great majority of cases is climatic unfitness. The quantity, distribution or interrelation of heat and moisture may be at fault. Thus, while the total quantity of heat may be adequate, the moisture may be inadequate, or the moisture may be adequate and the heat inadequate, or the quantities of heat and moisture may be too great or too small with respect to one another or to the time of year, and so on. What the farmer wants to know is *how to tell in advance* whether the climatic conditions on his own farm are fit or unfit for the particular crop he has in view, and what crops he can raise with reasonable certainty. It requires no argument to show that the answers to these questions would be worth in the aggregate hundreds of thousands of dollars yearly to the American farmer. The Biological Survey aims to furnish these answers."

Life-zone surveys upon the basis laid down by Merriam have been made by Bailey for Texas (1905) and New Mexico (1913), and by Cary for Colorado (1911) and Wyoming (1917). Robbins (1917) has made a somewhat similar study of the zonal relations in Colorado with reference to plants alone. Hall and Grinnell (1919:37) have recently published comprehensive lists of plants and animals which are regarded as "life-zone indicators" for California. As with Merriam's life zones, these are floristic and faunistic in character and hence do not necessarily correspond with community indicators.

Hilgard, 1906.—In summarizing his soil studies of more than 50 years, Hilgard formulated more fully and definitely his ideas of the indicator value of native vegetation. This account makes it clear that to Hilgard must be given the great credit of being the first to adequately realize the significance of indicators and to urge their inclusion in a basic agricultural method.

"The importance of the natural relations of each soil to vegetation is obvious, both from the theoretical and from the practical viewpoint. From the former, it is clear that the native vegetation represents, within the climatic limits of the regional flora, the result of a secular process of adaptation of plants to climates and soils, by natural selection and the survival of the fittest. The natural floras and silvas are thus the expression of secular, or rather millennial experience, which if rightly interpreted must convey to the cultivator of the soil the same information that otherwise he must acquire by long and costly personal experience.

"The general correctness of this axiom is almost self-evident; it is explicitly recognized in the universal practice of settlers in new regions of selecting lands in accordance with the forest growth thereon; it is even legally recognized by the valuation of lands upon the same basis for purposes of assessment, as is practiced in a number of States.

"The accuracy with which experienced farmers judge of the quality of timbered lands by their forest growth has justly excited the wonder and envy of agricultural investigators, whose researches, based upon incomplete theoretical assumptions, failed to convey to them any such practical insight. It was doubtless this state of the case that led a distinguished writer on agriculture to remark, nearly half a century ago, that he 'would rather trust an old farmer for his judgment of land than the best chemist alive.'

"It is certainly true that mere physico-chemical analyses, unassisted by other data, will frequently lead to a wholly erroneous estimate of a soil's agricultural value, when applied to cultivated lands. But the matter assumes a very different aspect when, with the natural vegetation and the corresponding cultural experience as guides, we seek for the factors upon which the observed natural selection of plants depends, by the physical and chemical examination of the respective soils. It is further obvious that these factors being once known, we shall be justified in applying them to those cases in which the guiding mark of vegetation is absent, as the result of causes that have not materially altered the natural condition of the soil. (p. XIX.)

"It was from this standpoint that the writer originally undertook, in 1857, the detailed study of the physical and chemical composition of soils. It seemed to him 'incredible' that the well-defined and practically so important distinctions based on natural vegetation, everywhere recognized and continually acted upon by farmers and settlers, should not be traceable to definite physical and chemical differences in the respective lands, by competent, comprehensively trained scientific observers, whose field of vision should be broad enough to embrace concurrently the several points of view—geological, physical, chemical, and botanical—that must be conjointly considered in forming one's judgment of land. Such trained observers should not merely do as well as the 'untutored farmer,' but a great deal better." (p. 315.)

This attitude toward plants and vegetation as indicators prevails throughout the book, and the subject is treated in considerable detail for the first time in Chapters XXIV to XXVI. These deal respectively with the recognition of the character of soils from their native vegetation, in Mississippi, and in the United States and Europe generally, and with the vegetation of

saline and alkali lands. While the author ascribes primary importance to the presence of lime, he does not fail to assign great value to water, especially in the West. He not only recognizes the indicator value of the presence of a particular species or group of species, but also takes into account the size, form, and development of the indicators. Significant tables and lists of indicators are given on pages 490, 497, 514-516, 518-519, and 536.

Clements, 1910.—In 1908, the work of the Botanical Survey of Minnesota was reorganized upon an ecological basis, for the purpose of making a classification and use survey of the lands of the State. The objectives of the survey were defined as follows (Clements, 1910:52):

"The first step in determining the final possibilities of Minnesota in plant production is to ascertain just what the conditions of soil and climate are from the standpoint of the plant. This must be determined separately for the two great groups of lands, those still unoccupied and those now in use. For the former, a knowledge of soil and climate and of the plant's relation to them is necessary to determine what primary crop, grain, forage, or forest is best. For the farms of the State, the best use is a matter of knowing the soil and climate differences of regions and fields, and of taking advantage of these in crop production. For the unoccupied lands of Minnesota, we need a classification survey to determine the best use of different areas, to prevent the waste of human effort and happiness involved in trying to secure from the land what it can not give and yet to insure that the land will reach as quickly as possible its maximum permanent return. For occupied lands, the study and mapping of soil and climatic conditions would constitute a use survey of the greatest value in adjusting plant production to the conditions which control it.

"The chief object of a classification survey is to group the unoccupied lands of the State as accurately as possible into three great divisions: (1) agricultural land, for crop production; (2) pasture land, for dairying and stock raising; (3) forest land, for lumbering, water regulation, and recreation parks. Such a division would be determined primarily by studies of soil and climate, necessarily supplemented by the evidence of native vegetation itself and of such cultivation as has been tried. The value of classification depends upon its accuracy, but the study of an area from these three standpoints neglects no source of evidence, and discloses practically all that can be learned of the possibilities."

The survey method was based upon the instrumental and quadrat study of habitats and communities, cultural as well as natural. The main divisions were vegetation mapping, the determination of indicators, and the study of succession. Vegetation and physiography were recorded on maps in which each division of 40 acres was represented by a square decimeter. Quadrat and transect charts were made of typical communities in each section of the township, and determinations of physical factors in all charted quadrats. The indicator work was devoted to the recognition of indicator species and communities so closely dependent upon water-content, soil, acidity, or light that they could always be used as indicating a certain set of conditions. Especial attention was given to the correlation of indicators with crop plants and with the secondary successions in burns, cutovers, fallow fields, pastures, roadsides, etc. Four townships were mapped upon this basis in 1912, and a large number of successional areas from 1913 to 1916. Some of the general

results have already been published (Bergman and Stallard, 1916; Stallard, 1916; Bergman, 1919; Stallard, 1919), while a part of the indicator findings are discussed later (Chapter XIII).

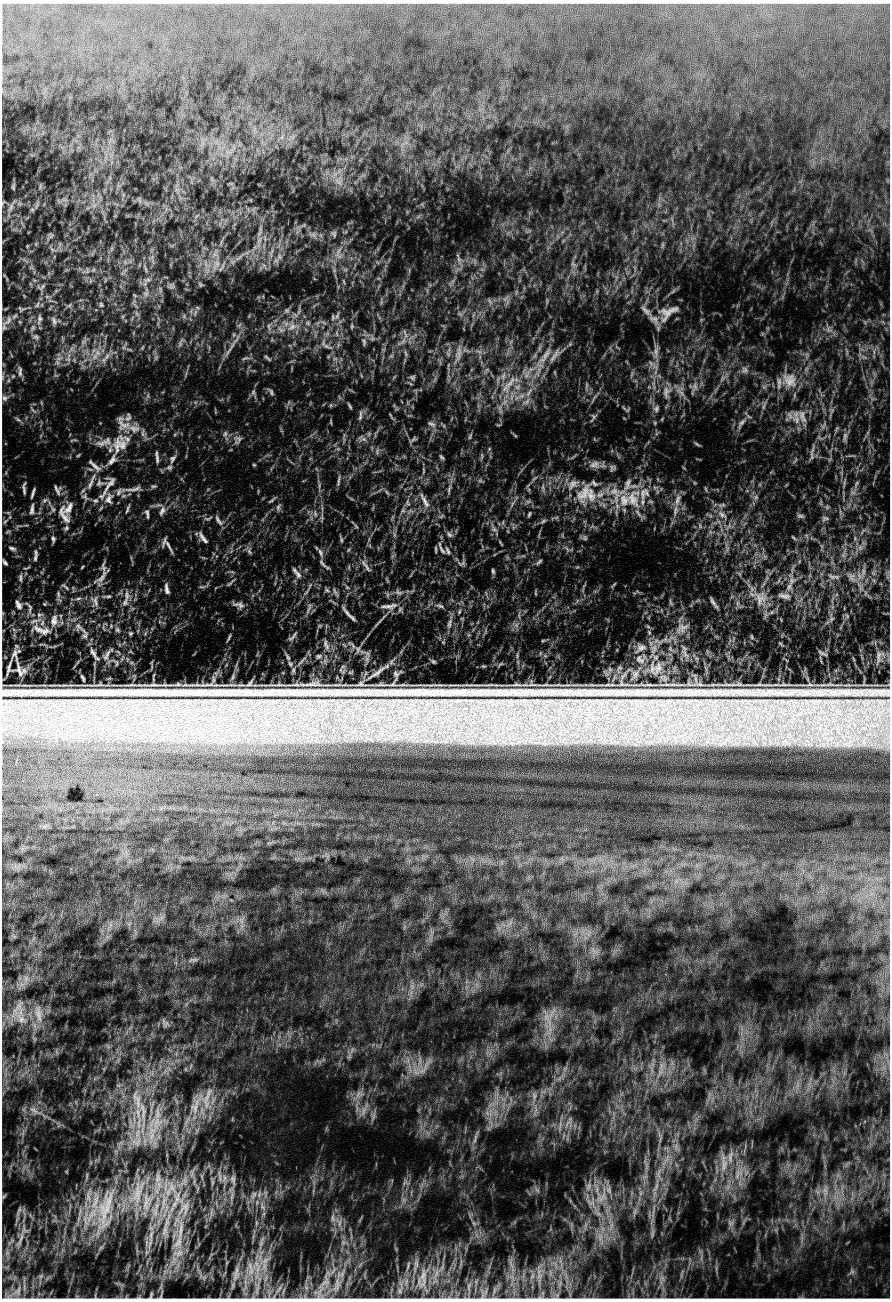
Shantz, 1911.—The study of the natural vegetation of the Great Plains by Shantz is the classic work on indicator plants. It was the first avowed investigation of indicators to be based upon the three cardinal points, namely, instrumentation, succession, and quadrats, and will long serve as the model for all thorough research in this field. Because of its great importance, the original should be consulted for the details. Here it must suffice to quote the author's general principles. (p. 9.)

"Farmers and other persons who have occasion to examine new land in order to form a judgment of its agricultural value depend largely upon the natural vegetation, or plant covering, as an indicator of its crop-producing qualities. But there are many possibilities of error in judging land upon this basis. Species that are closely related botanically and very similar in appearance may indicate quite different conditions of soil and climate. The popular names of plants are likely to cause confusion. Thus, the farmer who has learned in the Great Basin region that 'greasewood' is an indicator of alkali land and that 'sage-brush' usually grows on land free from alkali, will find if he moves to southern Arizona or southeastern California that the scrub there known as 'greasewood' indicates absence of alkali, while the so-called 'sage bushes' of that region grow on strongly alkali land. Furthermore, there is a general tendency to depend upon a single plant species as an indicator, while the investigations set forth in this bulletin show that the composition of the plant covering as a whole is a much more reliable basis for judging the crop-producing capabilities of land.

"The chief object of the present paper is to show how these sources of error may be avoided and how new land may be classified readily and with reasonable accuracy on the basis of its natural vegetation. This paper is not a report of a land survey, but rather a discussion of methods which it is believed could be utilized to advantage in making such a survey, the methods being illustrated by application to a limited territory in the Great Plains area.

"Too much emphasis can not be laid upon certain facts that have been clearly brought out in the course of these investigations: (1) Correlations between the natural plant cover and the crop-producing capabilities of land in a given area can be satisfactorily determined only after careful study of the different types of vegetation of the area in relation to their physical environments; (2) such correlations, determined for some particular region, will need to be modified to a greater or less extent before they can be applied in another region where the physical conditions are different. When, as a result of sufficient investigation, correlations of this nature are determined for a given area, it is believed that they will afford a basis for classifying the land of that area more readily and at least as accurately as by any other known method.

"In order to test and perfect the methods here described, it was necessary to make a detailed study of the vegetation of some particular area in relation to the physical conditions, checking the observations by the study of such examples of actual crop production as exist on the different types of land. It was decided to begin work in the Great Plains area, for this region contains the largest body of land in the United States having possible agricultural value on which the native plant covering is still undisturbed. A further advantage is the comparative uniformity of the climate throughout the area from the Canadian boundary on the north to the 'Panhandle' of Texas on the south. The investigations thus far have been made chiefly in a portion



A. Short-grass (*Bouteloua gracilis*) on hard-land, Colorado Springs, Colorado.
B. Wire-grass (*Aristida purpurea*) in short-grass subclimax, Walsenburg, Colorado.

of eastern Colorado, a region which is considered representative because of its central position and because its climatic conditions are almost as severe as anywhere in the Great Plains. But enough data have been gathered in other portions of the Great Plains to make it fairly certain that with comparatively little modification the correlations shown will hold throughout the area.

"The work so far accomplished has brought out clearly that in this area the general conditions, whether favorable or unfavorable to crop production, are indicated by the character of the native plant cover." (plate 24.)

Kearney, Briggs, Shantz, McLane, and Piemeisel, 1914.—The first quantitative study of plant communities as indicators of alkaline soils was made by Kearney and his associates in the Tooele Valley of Utah. This was essentially an application of Shantz's methods to a saline basin and met with similarly important results, as the following indicates:

"In the arid portion of the United States the different types of native vegetation are often very sharply delimited, the transitions being so abrupt that they can not be attributed to climatic factors; this has suggested the possibility of correlating the distribution of the vegetation with the physical and chemical properties of the soil. If such correlations can be made, they may be utilized in the classification of land with respect to its agricultural capabilities.

"One of the writers has described the correlations which exist in the Great Plains between the different types of vegetation and the physical characteristics of the corresponding types of land, and has pointed out how the native growth may be used in that region to determine the suitability of the land for dry-farming.

"The results obtained in the Great Plains made it desirable to undertake similar investigations in the Great Basin region. The problems to be solved were: First, what types of vegetation indicate conditions of soil moisture favorable or unfavorable to dry farming, and second, what types indicate the presence or absence of alkali salts in quantities likely to injure cultivated crops. For the purpose of this investigation it was necessary to find a locality where both dry farming and irrigation farming are practiced, where much of the soil is still covered with the original native growth, and where some of the soils contain an excess of alkali salts.

"After a reconnoissance trip through portions of Wyoming, Utah, Idaho, and Oregon in August, 1911, the Tooele Valley in central Utah was selected for the following reasons: (1) Several very distinct types of vegetation are found in a small area, (2) the soils show a great diversity in their moisture conditions and salt content, (3) the greater part of the area retains its original plant cover, while examples of crop production, both with and without irrigation, exist on different types of land.

"Detailed studies of the vegetation of Tooele Valley in relation to the moisture conditions and salt content of the soil were carried on in 1912. The work was begun near the close of the rainy season (end of May) and was terminated during the first week of August, when the summer drought had reached its height. Additional data were obtained during a third visit to the valley in the latter part of August 1913.

"The distribution of the native vegetation was found to depend in a marked degree upon the physical and chemical properties of the soils, factors which also influence crop production. So far as this particular area is concerned, the vegetation unquestionably can be used with advantage in classifying land with respect to its agricultural value. To what extent the correlations established in the Tooele Valley hold good in other parts of the Great Basin region remains to be determined by future investigation." (p. 365.)

The successional relations of the dominants have been discussed as well as graphically illustrated by Shantz (1916:234). The primary succession exhibits two adseres, one from *Salicornia* and *Allenrolfea* to *Artemisia*, and the other from *Allenrolfea* through *Distichlis* and *Sporobolus* to *Chrysothamnus*. These seral facts give much additional value to the indicator studies of the Great Basin, especially in establishing the indicator sequence and in imparting a distinct significance to the various mixed communities.

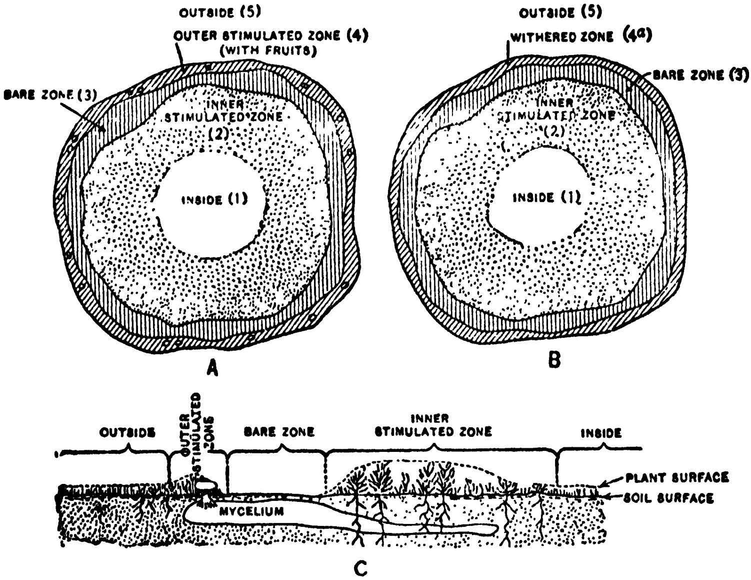


FIG. 10.—Zones of a fairy ring due to *Agaricus tabularis*: *A* and *C*, during a moist period; *B*, during a dry period. After Shantz and Piemeisel.

Shantz and Piemeisel, 1917.—In their exhaustive study of fairy rings in the Great Plains, Shantz and Piemeisel (1917:191) have shown the causal relation between the rings of mushrooms and grasses, as well as the indicator significance of the latter. They distinguish three types of fairy rings, based upon the effect shown by the vegetation: (1) those in which the vegetation is killed or badly damaged, caused by *Agaricus tabularis* (fig. 1); (2) those in which the vegetation is only stimulated, produced usually by species of *Calvatia, Catastoma, Lycoperdon, Marasmius,* etc.; (3) those in which no effect can be noted in the native vegetation, due to species of *Lepiota*. In the *Agaricus* rings, the vegetation shows three zones concentric to the central area of normal short-grass sod (1): the inner stimulated zone (2) is a broad one, differing in botanical composition, the more luxuriant growth, and the deeper green color from the center. The bare zone (3) is narrower and somewhat more irregular, while the vegetation is either dead or consists of a few very poor perennials or short-lived annuals. The inner zone is the most prominent feature of the ring in spring or wet seasons, the bare one in late summer or fall or in dry seasons. The outer stimulated zone (4) is rather narrow and is made up for most part of species peculiar to the short-grass sod, though resembling the inner zone somewhat. The mushrooms occur in the outer zone near the outside edge. In the case of most fairy rings, the

fungus produces a temporary stimulating effect only, and the ring is indicated merely by the increased size, vigor, and chlorophyll-content of the annuals and the perennial grasses.

The stimulation of the grasses and other plants which produced the inner and outer zones is probably due to the presence in the soil of nitrates and ammonia salts derived from (1) the reduction of the organic matter of the soil, (2) the decay of the mushrooms, and (3) the decay of the mycelium. The bare zone results from the death of the vegetation as a consequence of a lack of available soil moisture. Water penetrates very slowly into the sod filled with mycelium when it is once dry. The increased growth in the outer zone hastens the drying-out of the soil and, once dry, the latter is not wetted by heavy and continued rain. The vegetation is not noticeably damaged during growing seasons uniformly wet, but it quickly shows the effect of dry years or periods of drought. The secondary sere initiated by the fairy rings is essentially like that caused by any other disturbance in the short-grass association.

Shantz and Aldous, 1917.—In the field instructions for classifying public lands under the terms of the Stock Raising Homestead Act of 1916, Shantz and Aldous have made the most comprehensive use of indicators for the purpose of land classification. Ninety different types are recognized as indicator communities and are described briefly, though usually without a statement of the correlated conditions. Of these, 32 belong to the prairie-plains grassland climax, 20 to the sagebrush climax, 16 to the desert-scrub climax, and 9 to the chaparral. The types are designated by the names of dominants and subdominants and represent both seral and climax communities. Density, percentage of grasses and grass-like plants, and height of shrubs are also made use of for minor indications, while overgrazed areas are given especial attention. A key to correlation conditions and crop-producing capabilities was filed with the Geological Survey and is used by it in the interpretation of the types.

Weaver, 1919.—While the work of Shantz (1911), Weaver (1915), Sampson (1914, 1917), and of Cannon (1911, 1913, 1917), Markle (1917), and others had laid the basis for the consideration of root systems in connection with indicator values, the first special and comprehensive study of the indicator significance of roots was made by Weaver in 1918. This investigation derives its importance not only from the thoroughness of the methods, but especially also from the large number of species concerned, the wide range of the communities, and the consistency of the instrumental results. Approximately 160 species were investigated, involving the examination of about 1,150 individual plants. These were largely grasses and grassland herbs, but they included shrubs, undershrubs, weeds, and forest herbs as well. The communities represented were the prairies of Nebraska and the Palouse region of the Northwest, the short-grass plains and the sandhills subclimax of Colorado, the gravel-slide and half-gravel-slide associes, and the forest climax of the Pike's Peak region. In practically all these, readings were made of water-content, humidity, temperature, and light, and in critical ones of transpiration as well. In showing the community relations of competing root systems use was made of the quadrat-bisect. Many of the detailed results have been utilized in the discussion of particular indicators in Chapters XIV and XV.

FOREST INDICATORS.

A general idea of indicator plants has existed in forestry for nearly a century, and it is strange that the forester was not the first to formulate a system of indicators. His nearest approach to this is found in the tables of tolerance (Graves and Zon, 1911:20). The fact that the forester's attention was fixed primarily upon reproduction and little or not at all upon the shrubs and herbs of the forest floor probably explains the long absence of any definite recognition of indicators. In forestry as elsewhere, but even to a greater degree, a system of indicator plants and communities was impossible before the use of instruments and quadrats and the application of successional principles. As is shown later, however, forestry already possesses a large amount of indicator material which only needs to be organized upon a systematic basis. Practically all site studies have much and some of them great indicator value. However, the researches directed primarily toward this have been few, and it is necessary here to consider only the following:

Cajander, 1909.—Cajander (1909; Zon, 1914:119) has made an interesting endeavor to recognize forest types on the basis of the living ground-cover as indicators of the soil conditions. He classified the forests of Finland, composed largely of spruce, fir, beech, and oak, into three types:

1. *Oxalis* type (forests with a layer society of *Oxalis acetosella*).
2. *Myrtillus* type (forests with a layer society of *Myrtillus nigra*).
3. *Calluna* heath type (forests with a layer society of *Calluna vulgaris*).

The *Oxalis* type characterizes the best soils and comprises nearly all the dominant trees. It is further divided into four subtypes, marked by *Impatiens-Asperula, Asperula, Oxalis,* and *Oxalis-Myrtillus* respectively. As Zon points out, the dominant species of trees are assumed to play no part in determining the type. The author also dismisses the effect of light as of no importance. This appears to be quite unwarranted, as no measurements seem to have been made of light, as is apparently true of the other factors as well, and consequently the correlation between communities and conditions is superlatively general. Little or no attention is paid to the successional sequence of dominants or subdominants, and here again the real indicator values are overlooked or lost. Zon further points out that the author's own statements are contradictory, in that he states in one place that the layer societies indicate the physical conditions independent of the tree species, while in another the trees are said to determine the character of the herbaceous vegetation beneath them. While Cajander has naturally assigned greater importance to the subdominant herbs and low shrubs than to the dominant trees, his use of the forest societies as indicators is sound, and will serve to correct the usual practice of foresters who have neglected the undergowth.

Clements, 1910.—The investigation of the lodgepole-burn forests of northern Colorado in 1907-1908 was essentially a study of fire indicators, herbaceous as well as woody. Its real importance in this connection lay in the fact that it was the first study of forests made on the complete basis of instruments, quadrats, and succession. It was pointed out that lodgepole pine and aspen are practically universal indicators of fire and not of mineral soil or other conditions, at least for the Rocky Mountains. *Agrostis hiemalis, Chamaenerium angustifolium* and *Vaccinium oreophilum* were recognized as the chief

pioneers of the burn subsere, together with the mosses *Bryum argenteum* and *Funaria hygrometrica.* Several other species are almost equally good indicators of burns, especially when abundant. These are *Rubus strigosus, Carex rossii, Arnica cordifolia, Achillea lanulosa,* and *Anaphalis margaritacea.* The water and light factors for the six dominant trees were measured and the successional sequence thus obtained exhibits the indicator value of each species.

A successional study was made of the so-called natural parks of Colorado in 1910 for the purpose of determining their indicator significance as to reforestation, both natural and artificial. The conclusion was reached that all such grassland areas in forested regions are but seral stages leading to a forest climax. The majority of them are due to repeated burns or the slow filling of lakes, with the result that they persist as apparent climaxes for several hundred years. Their origin is readily disclosed by the indicators in them, as is also true of the rate of development.

Pearson, 1913-1914.—In discussing the proper basis for the classification of forest lands into types, Pearson (1913:79) has reached the following conclusions:

"The only scientific basis for such a classification is that of potential productiveness, considering both agricultural and forest crops. The productive value may be ascertained in two ways: The first measures directly, as far as possible, all physical factors on the site and gauges the productive capacity by the measure in which the sum of these factors meets the requirements of various crops. The second method uses characteristic forms of vegetation on the ground as an indicator of the physical conditions present, and upon this basis ascertains the adaptability of the site for different crops. The obvious objection to the first method is the need of climatological data and soil analyses on each site to be classified; and owing to the diversity of sites in our forest regions, together with the almost complete absence of climatological records in many sections, the collection of the needed data would involve an expense which, at this stage of our advancement in forestry, would be almost prohibitive. The second method requires a thorough preliminary investigation in each region to be covered, in order to secure a working knowledge for the actual land classification, and obviously reliable results can only be obtained by the employment of trained men. This method is the simpler and probably the more reliable of the two, and it is considered entirely applicable to the needs of the forester."

A general indicator relation is established between the five forest types and the agricultural possibilities of the Coconino National Forest in northern Arizona. The same author (1914:249) has employed seedlings of Douglas fir as indicators of the conditions for planting in aspen and in open situations at 8,700 feet on the south slope of the San Francisco Mountains. The seedlings were planted in two plots in the aspen and two in the opening each spring of the 3-year period, and instrumental readings were made of water-content, evaporation, wind, and temperature. The aspen uniformly gave a larger survival of seedlings than the opening, the percentage varying from 7 to 13. The critical factor in this was evaporation, which was 50 to 90 per cent higher in the open than under the aspen. The author further points out that the results indicate that yellow pine, because of its lower

moisture requirements and greater demands for light, will probably prove more suitable than Douglas fir for openings within the natural range of the former. A later study has dealt with the correlation of height-growth with precipitation, but this is considered under growth-forms in Chapter XII.

Zon, 1915.—At the suggestion of the writer, a conference was held at the Utah Forest Experiment Station in 1915 to discuss the feasibility of a system of indicators for silvics and grazing, and especially the indicator value of shrubby and herbaceous species and communities, with particular reference to succession. The conference consisted of Mr. Zon, chief of silvics, Mr. Jardine, inspector of grazing, Dr. Sampson, director of the station, Dr. E. S. Clements, and the writer. There was general agreement upon the value of indicators as a basis for the experimental regeneration of forest and grassland. As an outcome, Mr. Zon drew up a preliminary outline of the indicator significance of the important dominants of the various zones and represented this graphically in a schematic transect (fig. 25). This appears to have been the first definite organization of the indicator experience of the Forest Service in silvical work. Its proposals as to indicators are considered in Chapter XVI.

A similar conference on indicators and succession was held at the station in 1917. It was attended by Professor Toumey, Professor Pool, Dr. E. S. Clements, Dr. Sampson, Mr. Korstian, Mr. Baker, Mr. Weil, and other members of the staff, together with the writer. Particular attention was given to seral indicators of grazing burns, erosion and slides, as well as to climatic indicators in the chaparral belt. Some of the conclusions are to be found in the discussion of indicator papers in Chapter XVI, as well as in the body of the text itself.

Hole and Singh, 1916.—In studying the reproduction of sal (*Shorea robusta*) in the forests of India, Hole and Singh have made a quantitative study of the water and light factors that control germination and ecesis. Their work is especially noteworthy in that experimental quadrats have been employed for the analysis of different sites (p. 48), and that a detailed study was made of soil aeration as a critical factor. The general indicator results are given in the following excerpts:

"Broadly speaking three principal soil types may be distinguished in these areas, and these are characterized by different types of vegetation, as follows:

A. Containing a large percentage of sand and a relatively small percentage of the finer particles of silt. The soil is also frequently shallow, with gravel and boulders below, and is therefore essentially dry.

Dry miscellaneous forest with *Acacia catechu* and *Dalbergia sissoo* prominent, or grassland with *Saccharum munja* dominant.

B. Sal forest or grassland, well aerated deep loam with *Saccharum narenga* (often mixed with *Anthistiria gigantea arundinacea*) dominant.

C. Badly aerated deep loam. This differs from (B) either in containing more clay and silt, in being actually denser with less pore space per cubic foot, or in having the water-table nearer the surface.

Moist miscellaneous forest with *Butea frondosa, Stereospermum suaveolens, Terminalia, Cedrela toona* and others, or grassland with *Erianthus ravennae* (often mixed with *Anthistiria gigantea villosa*) dominant.

"One of these types is unsuitable for the growth of sal, inasmuch as the water-content of the soil falls rapidly to the death-limit after the close of the rainy season, while another type is unsuitable on account of bad soil-aeration

which leads to a low percentage of germination, a high percentage of deaths during the rains, and a superficial root system. The latter point is of great importance, inasmuch as it leads to the roots being situated in those layers of soil the water-content of which is reduced to the death-limit in the dry season. It will thus be seen that the results obtained go far to explain the natural distribution of sal, and also indicate those grasslands and forestless areas in which afforestation with sal offers the greatest chance of success. Finally, it has been shown that, owing chiefly to the heavy shade, the aeration of the superficial soil layers in dense sal forest is commonly below the death-limit for several weeks during the rains and that this factor is responsible (1) for the holocaust of sal seedlings which takes place during the rains in shady forests in years of heavy rainfall and (2) for the development of a superficial root system which, in the hot season when the sal sheds its leaves and the forest canopy thins out, leads to widespread damage from drought among those plants which survive the rains. Opening of the cover and temporary removal of the humus are obvious expedients by means of which the soil-aeration can be improved. Firing would also in some cases probably be beneficial in this respect." (p. 38.)

"It will be seen that the management of any particular sal forest to a great extent depends on the fact whether the seedlings in it suffer chiefly from drought or from bad soil-aeration and therefore the determination of this point is of primary importance. Observations regarding the season when the seedlings chiefly die and the dryness of the soil at the time naturally indicate to a great extent which factor is primarily concerned. In addition to this, however, the work which has been carried out at Dehra during the last few years has shown that the dominant grasses on an area are, as a rule, excellent indicators of the soil conditions. Thus in northern India, where *Saccharum narenga* and *Anthistiria gigantea arundinacea* tend to be dominant, the soil moisture and aeration are as a rule suitable for the best development of sal, and sal forests of the moist type prevail. In shady forest in such localities, the seedlings suffer chiefly from bad soil-aeration and the most efficient remedy consists in opening the cover and exposing the soil. On the other hand, such grasses as *Saccharum munja, S. spontaneum, Eragrostis cynosuroides, Imperata arundinacea, Vetiveria zizanoides, Andropogon contortus,* and *Ischæmum angustifolium* usually indicate a soil too dry or too dense for the best sal development, and such forests as occur are of the dry sal type. The recognition of the dominant grasses in the sal tracts therefore is a matter of considerable practical importance, and a subsequent paper will deal in more detail with the grasses of the sal tracts, in their capacity as soil indicators." (p. 83.)

Korstian, 1917.—In a study of permanent quadrats on the Datil National Forest of New Mexico, Korstian (1917:267) gives the increment data for *Pinus ponderosa* on sites I and II, and points out that the growth of a dominant tree is the best indication of the quality of forest sites. The differences in the native vegetation on the two sites were so great as to suggest its correlation with tree-growth and its use as an indicator of forest sites. A large number of list quadrats were employed, but the lack of previous successional studies makes their accurate interpretation difficult and probably explains in part the conclusion that

"In studying the indicator significance of the native vegetation it is necessary to go directly to the individual species instead of attempting to stop at the association, society, or community.

"The writer believes that the native vegetation found on deforested areas

may be considered as a criterion of the latent potentialities of the site for forest production provided the vegetation has not been too seriously or too recently disturbed and that the more important phases of the successional series are properly understood.

"The fundamental study of forest planting sites logically resolves itself into three categories: (1) The empirical establishment of plantations and the observation and study of their survival and subsequent development; (2) the measurement and study of the most important physical factors of the site, such as the available soil moisture or growth water and evaporation; and (3) the indicator significance of the native vegetation occurring on the sites, implying a very careful correlation of all three phases.

"It is readily conceivable that site studies of this character will be of the utmost value in explaining the presence or absence of tree growth on certain areas, in the judicious selection of the proper species and sites in the reforestation of much of the denuded forest land of the United States, and in establishing a working basis for the classification of forest lands. Only after considering the relative agricultural and forest productivity of the land on a combined scientific and economic basis, can a positive conclusion be reached that its greatest utility lies in its use for forestry or for agricultural purposes."

GRAZING INDICATORS.

Grazing has been recognized as a distinct field for investigation for scarcely more than a decade. Complete recognition of grazing as a subject for experiment should perhaps be dated from the establishment of the Utah Forest Experiment Station for grazing in 1912. Three more or less marked steps in advance had preceded this and had made it inevitable. The first was a general study of the West with reference to the species, distribution, and value of the native grasses and forage plants. The stimulus for this seems to have been the work of Bessey in Nebraska, as indicated by the publication of many reports dealing with grasses and forage plants from 1886 to 1907. Webber (1890), Smith (1890), and Williams were associated with Bessey in some of this work and the last two later carried on extensive grassland studies over the Great Plains and the Rocky Mountain region (Smith, 1898; Williams, 1897, 1898). Similar studies were made by Clements in 1893, Shear and Clements in 1896, by Rydberg and Shear in 1897, by Pammel in 1897, Nelson in 1898, and others (cf. Shear, 1901). The second step was perhaps the most significant, inasmuch as it introduced the quantitative study of grazing areas by means of the quadrat, and provided an exact method of measuring carrying capacity and determining the degree of overgrazing or the amount of regeneration. This work was begun by Griffiths and Thornber in 1901 and enlarged in 1903 on what is now the Santa Rita Grazing Reserve of the Forest Service. It has been carried on continuously since that time by Griffiths, Wooton, Thornber, Hurtt, and Hensel in turn, and this now constitutes the classic field for grazing study anywhere in the world. It has yielded publications of primary importance by Griffiths (1901, 1904, 1907, 1910), Thornber (1910), and Wooton (1916). Somewhat similar lines of experiment were begun by Coville and Sampson in 1907 in the Wallowa National Forest in northeastern Oregon. The results are recorded in a series of reports of unusual significance, namely, Sampson (1908, 1909, 1913, 1917) and Jardine (1908).

The third period of rapid development in grazing studies began with the organization of grazing reconnaissance in the six districts of the Forest Serv-

ice in 1911. During the past seven years reconnoissances have been made on practically all of the National Forests, and the grazing upon these has been administered upon the basis of a definite carrying capacity. The result has been to favor regeneration to such an extent that most of the ranges have recovered their normal carrying capacity to a large degree. With the extensive work in reconnaissance went the establishment of permanent quadrats, especially in the Coconino, Targhee and Deerlodge National Forests. Those on the Coconino especially have been actively studied (plate 42A), and have already yielded results of much value (Hill, 1917).

The most signal advance has been marked by the organization of a grazing experiment station of the Forest Service at Ephraim, Utah, in 1912. This has been followed by the establishment of experimental pastures for grazing at Mandan (North Dakota), and Ardmore (South Dakota), by the Office of Dry Land Agriculture of the U. S. Department of Agriculture. Somewhat earlier than this, in 1908, Marsh had begun experimental work in Colorado on poisonous plants, and this is now carried on at a special experiment station at Salina, Utah, on the Fishlake National Forest. In 1914, the Jornada Grazing Reserve was established near Las Cruces, and this, like the Santa Rita Reserve, is essentially a grazing experiment station in the open range country. It seems inevitable that the organization of grazing reserves and experiment stations will proceed rapidly until they are found in all the important grazing types of the country, as well as in each State, including the South. An account is given in Chapter XV of the inauguration of a comprehensive system of grazing investigations throughout the West during 1917-1919.

Practically none of the grazing studies abstracted in the following pages was intended to deal with indicator plants. In spite of this fact, however, they all contribute more or less definitely to the understanding of grazing indicators, because of the simple and direct relation grassland dominants and subdominants have to grazing. In addition, the abstracts furnish a fairly complete outline of the progress of grazing investigations during the past twenty years.

Smith, 1899.—The first clear recognition of grazing as a fundamental field for investigation was accorded by Smith in his study of grazing problems in the Southwest. His paper is a mine of valuable suggestions, and foreshadows a large number of the later experiments. The author has a distinct idea of grazing indicators and of succession, as the following excerpts show:

"Before the ranges were overgrazed the grasses of the red prairies were largely bluestems or sage grasses (*Andropogon*), often as high as a horse's back. After pasturing and subsequent to the trampling and hardening of the soil, the dog grasses or needle grasses (*Aristida*) took the whole country. After further overstocking and trampling, the needle grasses were driven out and the mesquite grasses (*Hilaria* and *Bulbilis*) became the most prominent species. The occurrence of any one of these as the dominant or most conspicuous grass is to some extent an index of the state of the land and of what stage in overstocking and deterioration has been reached.

"There is often a succession of dominant grasses in nature through natural causes, but never to so marked an extent as on the cattle ranges during the process of deterioration from overgrazing. Thus, the grasses in any given valley are liable to change in a long series of years through destruction by wood

lice, prairie dogs, by fires, unusually early or late frosts, or by failure on the part of the plant to ripen seed. This later contingency frequently occurs in the case of the big bluestems and the feather sedge, and probably with some others of the *Andropogon* species. The curly mesquite will stand almost any amount of drought, trampling, and hard usage, but is easily killed and rotted out during a wet cold winter. The drought-resistant needle grass is frequently destroyed by wood lice over considerable areas. This usually happens in the spring on burned areas after light local showers. Fnally, the entire seed crop may be destroyed by early autumn fires. Thus it is seen that through some one of many natural causes a species of grass may be all but exterminated and its place taken by others, often of less value.

"On overstocked land there is uniformly an alternation of needle grass and mesquite at short intervals, unless the overstocking is carried too far, when these perennials give way to annuals and worthless weeds. The carrying capacity then depends almost absolutely on the proper distribution of rainfall through the growing season in order to bring this transient vegetation to its fullest maturity." (p. 28.)

The text is divided into the following heads: (1) investigation of carrying capacity, (2) destruction of grasses by animal pests, (3) deterioration through increase of weeds, (4) renewing the cattle ranges, (5) rest versus alternation of pastures, (6) additional aids to range improvement, (7) grazing regions in Texas and New Mexico, (8) relation of land laws to range improvement, and (9) benefits of improving the ranges. The most significant part of the report is that which has to do with the regeneration of the range by means of rotation pastures. Experimental sections were selected at Abilene and Channing, Texas, representing prairie and plains respectively. On these the following experimental pastures and areas were established (p. 20; Bentley, 1902:15).

Pasture No. 1 (80 acres): No treatment except to keep all stock off until June 1 of each year, pasturing the balance of the season.

Pasture No. 2 (80 acres): To be cut with a disk harrow, and stock to be kept off until June 1 of each year, pasturing the balance of the season.

Pastures Nos. 3 and 4 (40 acres each): To be grazed alternately, the stock to be changed from one pasture to the other every two weeks, thus allowing the grasses a short period for recovery after each grazing.

Pasture No. 5 (80 acres): No treatment except pasturing until June 1 and keeping stock off the balance of the season.

Pasture No. 6 (80 acres): No treatment except to keep stock off during the first season.

Pasture No. 7 (80 acres): To be harrowed with an ordinary straight-toothed harrow and stock kept off during the first season.

Pasture No. 8 (80 acres): To be disked and stock kept off during the first season.

Pasture No. 9 (70 acres): Reserved for special experiments, viz., to determine (1) whether or not seeds of a number of wild and cultivated varieties of grasses and forage plants, exclusive of the grasses, could be sown directly in the sod with satisfactory results. (2) Whether the roots of certain sod and pasture grasses could be transplanted to the bare spots and a good stand secured in that way. (3) Whether the stand of grass could be improved by opening furrows across the pasture, in which the grass seeds blown over the ground by the winds could be arrested and the stand of grass be improved.

Bentley, 1902.—The preceding experiments, though initiated by Smith, were carried out by Bentley from 1898 to 1901. His results are of great value as the first outcome of actual and successful experimentation in improving the range. At the beginning the maximum carrying capacity of the area was

determined to be 16 acres per head, or 1 : 16. During the first year, the carrying capacity was estimated to have increased to 1 : 8, or 100 per cent. Unfortunately, no detailed report was made on the different pastures, and it was impossible to tell whether rotation or disking and harrowing was of the greater value in securing these results. At the end of the second year, a further improvement of 30 to 50 per cent was noted in the disked pastures. By the close of the three-year period, while the whole area had improved more than 100 per cent, the greatest improvement was noted in the pastures which had been disked and harrowed. Two minor experiments of much practical interest were also carried out successfully. The one consisted of plowing furrows 12 feet apart over 10 acres of pasture 9. The many fruits caught in the furrows germinated readily and grew vigorously because of the increased water-content. The latter also benefited the grasses between the furrows. The other test involved the transplanting of grass mats and bunches for the purpose of covering bare areas in prairie-dog towns and other denuded areas. The results are of especial significance and are further discussed in Chapter XV.

Griffiths, 1901, 1904, 1907, 1910, 1915.—Griffiths's work upon the grazing ranges of southern Arizona from 1903 to 1910 is entitled to great credit as the earliest consistent study of range production. The quadrat method was employed more or less, and some attention was paid to physical factors and incidentally to changes of population. The objects of the investigation were (1) to demonstrate that run-down and overstocked ranges will recover under proper treatment, (2) to ascertain how long a time is necessary to get appreciable and complete recovery, and what methods of management will produce such results, (3) to carry on reseeding and introduction experiments in the hope of increasing the total quantity of feed, (4) to measure as accurately as possible the carrying capacity of a known representative area. The report of 1915 on the native pasture grasses of the United States contains a large amount of valuable material with direct bearing upon grazing indicators.

The general results of the investigations are shown by the following summary (1910:24):

"The lands under consideration appear to regain their original productivity in approximately three years of complete protection.

"Evidence thus far secured seems to indicate that the best lands in the vicinity will improve under stocking at the rate of one bovine animal to 20 acres. The poorer lands take a correspondingly larger acreage for each animal. The areas that will carry one head to 20 acres are very limited.

"Brush and timber are encroaching upon the grasslands, due, it is believed, to protection from fires.

"A ground cover is not a factor below an altitude of about 3,500 feet.

"Although the maximum yield of forage may be reached in about three years of protection, improvements in quality of forage will probably go on longer through the continued supplanting of annual plants by perennials of greater value.

"Thus far alfilerilla is the only introduced plant which has succeeded and this only in the most favored situations. It does not appear to thrive in competition with the native perennial grasses at those altitudes where the latter are not grazed.

"None of the other 200 lots of seed sown has given any promise of success

except those of three or four native species. These give beneficial results, but the cost is high.

"Results seem to be secured much more rapidly through proper protection from overgrazing than by any other method."

Sampson, 1908, 1909, 1913, 1914.—The series of reports by Sampson on revegetation in the Wallowa National Forest constitute a contribution of the first importance to the science of grazing. They likewise furnish a large amount of experimental data as to grazing indicators in the montane and subalpine zones. The general results (1914:146) are applicable to a wide range of grasslands and are summarized below. They not only take into account the need of thoroughgoing and extensive studies of quadrats, factors, and succession, but they also consider in detail the ecological requirements of the various species.

"(1) Normally the spring growth of forage plants begins in the Hudsonian zone about June 25. For each 1,000 feet decrease in elevation this period comes approximately 7 days earlier.

"(2) In the Wallowa Mountains the flower stalks are produced approximately between July 15 and August 10, while the seed matures between August 15 and September 1.

"(3) Even under the most favorable conditions the viability of the seed on summer ranges is relatively low.

"(4) Removal of the herbage year after year during the early part of the growing season weakens the plants, delays the resumption of growth, advances the time of maturity, and decreases the seed production and the fertility of the seed.

"(5) Grazing after seed-maturity in no way interferes with flower-stalk production. As much fertile seed is produced as where the vegetation is protected from grazing during the whole of the year.

"(6) Germination of the seed and establishment of seedlings depend largely upon the thoroughness with which the seed is planted. In the case of practically all perennial forage species, the soil must be stirred after the seed is dropped if there is to be permanent reproduction.

"(7) Even after a fertile seed crop has been planted there is a relatively heavy loss of seedlings as a result of soil heaving. After the first season, however, the loss due to climatic conditions is negligible.

"(8) When 3 years old, perennial plants usually produce flower-stalks and mature fertile seed.

"(9) Under the practice of year-long or season-long grazing, both the growth of the plants and seed production are seriously interfered with. A range so used, when stocked to its full capacity, finally becomes denuded.

"(10) Year-long protection of the range favors plant growth and seed production, but does not insure the planting of the seed. Moreover, it is impracticable because of the entire loss of the forage crop and the fire danger resulting from the accumulation of inflammable material.

"(11) Deferred grazing insures the planting of the seed crop and the permanent establishment of seedling plants without sacrificing the season's forage or establishing a fire hazard.

"(12) Deferred grazing can be applied wherever the vegetation remains palatable after seed maturity and produces a seed crop, provided ample water facilities for stock exist or may be developed.

"(13) The proportion of the ranges which should be set aside for deferred grazing is determined by the time of the year the seed matures. In the

Wallowa Mountains, one-fifth of the summer grazing season remains after the seed has ripened, and hence one-fifth of each range allotment may be grazed after that date.

"(14) The distribution of water and the extent of overgrazing will chiefly determine the area upon which grazing should first be deferred.

"(15) After the first area selected has been revegetated, it may be grazed at the usual time and another area set aside for deferred grazing.

"This plan of rotation from one area to another should be continued, even after the entire range has been revegetated, in order to maintain the vigor of the forage plants and to allow the production of an occasional seed crop."

Jardine, 1908, 1909, 1910, 1913.—Jardine has made a careful study of the relation of coyote-proof pastures to carrying capacity, and finds that the latter is nearly 100 per cent greater than under the usual method of herding in large bands. This is due to the fact that the sheep graze much more openly and do much less trailing, with the result that the vegetation is trampled very much less (1908:31, 1909:38).

The establishment of grazing reconnoissances on the six forest districts and the organization of a method by Jardine in 1911 marked the beginning of an adequate system of grazing on the National Forests. This work has yielded a large number of facts of importance in connection with grazing indicators. Although it has never been published, its value is such as to warrant a brief abstract of it here. The main object of the reconnoissance was to secure a map classifying all the land of each National Forest into grazing types, and the location of each type, its carrying capacity and nature, whether winter, summer, or year-long range. The field notes dealt with the dominant species of each type, the density of ground cover expressed in tenths, the degree of utilization, and the presence of poisonous plants and range-destroying animals. Of most interest to the student of indicator plants is the system of types and subtypes which is outlined below. As quadrats gradually came into use in connection with reconnoissance, the later is now intensive to some degree in its methods.

Type 1. Open grassland other than meadow and secondary meadow.
Subtypes: bunch-grass, grama grass.
Type 2. Meadows.
Subtypes: wet meadow, dry or secondary meadow.
Type 3. Weed.
Type 4. Browse.
Type 5. Sagebrush.
Type 6. Timber, with a cover of grasses, weeds, and browse.
Subtypes: pine-grass, weeds, browse.
Type 7. Waste range.
Subtypes: waste timber, waste brush.
Type 8. Barren land.
Type 9. Woodland.
Type 10. Aspen.

Wooton, 1915, 1916.—In his discussion of the factors affecting range management in New Mexico, Wooton (1915:20, 23) has touched incidentally upon grazing indicators. The bulletin on the carrying capacity of ranges in southern Arizona (1916) continues the studies carried on by Griffiths from 1903 to 1910. Five associations are recognized, and an interesting account is given of the secondary succession following plowing in the crowfoot-grama and the six-weeks grass communities. Of especial interest is the account of carrying capacity as determined by cut-quadrats, and by actual grazing tests in the various pastures. The conclusions are grouped under the following heads:

Recovery.—The revegetation above 3,200 feet had become marked in about

three years after fencing. This improvement has continued, but more and more slowly each year, indicating that the normal condition is being reached. Below 3,200 feet, the rate of recovery has been slower and hence it should continue for a longer period. Three years of complete protection gave about three-fourths of complete recovery for the crowfoot-grama consociation with an annual rainfall of 15 to 18 inches. After 11 years the grazed areas are but partially recovered, though their carrying capacity has increased about 30 per cent.

Reseeding.—Practically all attempts to introduce new species of forage plants or to increase the abundance of endemic species beyond the normal have failed. Alfilaria and some aggressive annuals have given promise, but in the course of a few years the native perennials have crowded them out.

Carrying capacity.—This has been determined by means of cut-quadrats, hay-cutting, mapping the communities, and by grazing tests of the best part of the reserve. For the latter, the carrying capacity is 14 acres per head, while it is 20 acres for the whole reserve. One of the pastures stocked on the basis of 58 acres per head was not noticeably different in condition from adjacent land protected for 11 years, thus indicating a utilization below 50 per cent.

Jardine and Hurtt, 1917.—In the account of the results obtained on the Jornada Grazing Reserve from 1912 to 1917, Jardine and Hurtt have embodied the essentials of the first complete grazing system based upon actual experimental study of the herd as well as of the range. As a consequence, it serves as an excellent model for all ranches large enough to permit the rotation system of pastures and to warrant the segregation of herds by ages and classes. Taken in conjunction with the more intensive grazing experiments such as have been carried on by Sarvis (1919) at Mandan, it furnishes a complete experimental method of range studies. It is especially important in demonstrating how much experimental work and resulting improvement of range and herd can be carried on even under existing economic conditions on well-managed ranches (plate 36, A).

The authors' most important conclusions are as follows:

The grama-grass range has improved at least 50 per cent in the three years, compared with adjoining unfenced range grazed yearlong. This has been secured by reducing the number of stock during the main growing seasons from July to October to about half the average number the area will carry for the year, by refraining from overstocking during the other eight months and by better distribution of watering places. The range thus lightly grazed during the growing season has apparently improved as much as similar range protected during the whole year. Where the whole of a range unit is grama, about one-third should be reserved in rotation for light grazing during the growing season for two successive years.

Fairly efficient utilization of the range is secured by watering places with a 2.5 mile grazing radius. When the distance is greater than this, serious overgrazing or actual denudation occurs around the well or tank, while the remote areas are but partially utilized. The carrying capacity of the grama grass is 20 to 30 acres, of the tobosa grass 38 to 45 acres, and of the mountain range 60 acres. This is based upon carrying stock through the average year in good condition, and feeding the poorer stock concentrates to eliminate loss from starvation at critical periods.

Jardine and Anderson, 1919.—In an account of range management on the National Forests, Jardine and Anderson (1919:17) have discussed briefly the general indicators of overgrazing:

"Overgrazing for an extended period will leave 'earmarks,' which usually will be recognized. To recognize current overgrazing at the time of examination on a range previously not overgrazed is difficult and yet important in order to make timely adjustment. The following obvious earmarks are the most reliable indicators of overgrazing prior to the year of examination:

"*The predominance of weeds and grasses* such as knotweed (*Polygonum* spp.), tarweed (*Madia* spp.), mustard (*Sophia incisa*), annual brome grasses (*Bromus hordeaceus, brizaeformis, tectorum*), and fescues (*Festuca megalura, microstachys, confusa*), with a dense stand of such species and lack of variety in species. This condition is a severe stage of overgrazing such as occurs around sheep bedding grounds which have been used for long periods each year for several years in succession.

"*The predominance of plants which have little or no value for any class* of stock, such as sneezeweed (*Dugaldia hoopesii*), niggerhead (*Rudbeckia occidentalis*), yellowweed (*Senecio eremophilus*), snakeweed (*Gutierrezia sarothrae*) and gumweed (*Grindelia squarrosa*). These and similar plants frequently occur in abundance over large areas of range and indicate that the range needs careful management to give better forage plants a chance to grow.

"*The presence of dead and partly dead stumps of shrubs,* such as snowberry (*Symphoricarpos oreophilus*), currant (*Ribes* spp.), willow (*Salix* spp.), service berry (*Amelanchier* spp.), birch-leaf mahogany (*Cercocarpus montanus*), and Gambel oak (*Quercus gambellii*). This condition usually indicates that the most palatable grasses and weeds have been overgrazed. There may be some exceptions to this, as in the case of dwarfed willows on ranges where grasses predominate above timber line. Sheep sometimes kill the willows before the grasses are overgrazed.

"*Noticeable damage to tree reproduction,* especially to western yellow-pine (*Pinus ponderosa*) reproduction on sheep range and aspen (*Populus tremuloides*) reproduction on cattle range. Lack of aspen reproduction on a weed sheep range indicates overgrazing, provided the natural conditions are favorable to aspen reproduction. On a sheep range where grass predominates severe injury to western yellow-pine or aspen reproduction may indicate that the range is not well suited to sheep.

"The earmarks described are, perhaps, more typical of overgrazed sheep range than of overgrazed cattle range, but the general appearance of the two does not differ greatly when overgrazing reaches a stage to be recognized by one or more of these earmarks. The main differences are in the species of plants indicating the overgrazing. Weeds eaten by sheep are often found in abundance on overgrazed cattle range; coarse grasses palatable to cattle are often abundant on overgrazed sheep range. This fact has given rise to the use of the term 'class overgrazing.' "

Sarvis, 1919.—The first adequate intensive experiments in grazing have been carried on by Sarvis (1919) at Mandan, North Dakota, since 1916, and at Ardmore, South Dakota, since 1918. These have dealt primarily with carrying capacity and rotation grazing, though a number of related problems have been taken into account, such as rate of growth, effect of mowing, etc. The experiments are based upon actual grazing tests to determine the present carrying capacity of a particular type and the optimum utilization resulting from rotation. At Mandan, for example, the carrying capacity tests comprise

four fields of 30, 50, 70 and 100 acres respectively, each grazed by 10 animals of the same age and class. These are weighed at frequent intervals and the carrying capacity expressed in terms of pounds gained in weight. There are three rotation pastures to permit grazing during one-third of the growing season—spring, summer, and fall respectively. The behavior of the community under the different degrees and kinds of grazing is measured by means of an unusually complete system of chart- and clip-quadrats. The details of the method are discussed in Chapter XV.

CHRESARD AND WATER REQUIREMENT STUDIES.

Significance.—While practically all studies of the chresard or available water in soils have been made without definite reference to indicator plants, it is clear that they have a direct bearing upon the latter. This is likewise true of researches upon water requirements, especially those that relate to controlling physical factors. Since the value of an indicator depends upon the exactness of its correlation with direct factors, and especially water, it is often totally misleading to relate it to obvious or superficial facts. For this reason a scientific system of indicators has but recently become possible. It was a distinct step in advance to connect species with the total water-content or holard. But this gives trustworthy results only for the same soil. To obtain exact results it has become necessary to determine the water-withholding power of different soils and the water-using capacity of different plants. It has likewise proved imperative to take into account the salt-content and air-content of the soil solution. In the further analysis of indicators, it proves desirable to utilize their form, growth, and abundance for more minute and exact values. Hence a knowledge of the growth requirements, which are largely water requirements, has come to be highly significant.

Much work has been done upon the chresard of different soils and plants, and a still larger amount upon water requirements. Most of the former is American, and has been done in the West. As a result, it has a direct bearing upon the problem under consideration here. Of the great mass of water requirement data only a few deal with native or non-cultivated species, and are pertinent to the present discussion. For these reasons a concise account is given of the progress of the chresard concept.

The chresard.—The earliest studies of the water-content non-available to plants were incidental and failed to recognize the fundamental importance of the distinction.

Sachs (1859, 1865:173) found that a young tobacco plant began to wilt in a mixture of sand and beech mold at 12.3 per cent and that the chresard for this soil was 33.7 per cent. A second plant in clay wilted at 8 per cent, with a chresard of 44.1 per cent, while for a third the echard in sand was 1.5 per cent and the chresard 19.3 per cent. Heinrich (1874) determined the echard of barley in peat as 47.7 per cent and of rye as 53.4 per cent. In calcareous soil corn wilted at 8.6 per cent and broad beans at 12.7 per cent. Mayer (1875) observed that pea plants wilted at 33.3 per cent in sawdust, 4.7 per cent in marl, and 1.3 per cent in sand, while Liebenberg found that beans wilted in loam at 10 per cent, in marl at 6.9 per cent, and in coarse sand at 1.2 per cent.

Gain, 1895.—Gain (1895:73) has studied the behavior of three mesophytes in six different soils, with the results indicated in the table below. The echard varies less than 50 per cent for these species in any one of the first three soils, but the variation rises as high as 60 to 130 per cent in the last three. Part of this may be due to a larger error in determining the low echard. The author concludes that species not only wilt at different points, but also that this varies for different stages of the development of the same species.

Soils.	Erigeron canadensis.		Phaseolus vulgaris.		Lupinus albus.	
	Echard.		Echard.		Echard.	
	I.	II.	I.	II.	I.	II.
	p. ct.	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
Heath soil.	9.26	9.40	10.73	10.60	10.90	11.10
Clay	7.73	7.78	9.73	9.58	11.50	11.35
Humus ...	6.80	6.83	6.10	5.92	6.86	6.95
Lime soil..	4.19	4.25	2.94	2.90	5.15	5.23
Garden soil.	2.30	2.40	1.79	1.88	2.82	2.91
Sand	0.45	0.48	0.33	0.35	0.76	0.75

Kihlmann (1890 : 105) was probably the first to perceive the ecological significance of the echard, in connection with his studies of water relations in the frozen bogs of Lapland. However, Schimper first recognized the universal application of the concept and formulated it definitely as follows (1898:3; 1903:2):

"It is necessary to distinguish between physical and physiological dryness and wetness; the physiological water-content alone is important for plant-life and hence for plant-geography."

Neither Kihlmann nor Schimper appears to have made actual determinations of the physiological water-content. Clements (Pound and Clements, 1900:167; Clements, 1904:23; 1905:30; 1907:13; 1916) developed methods for determining the echard and chresard in the field as well as under control. These were applied to various habitats in the prairie and woodland regions of Nebraska, and on Pike's Peak in Colorado. The general results were in accord with those of the earlier investigators, Sachs, Gain, and others, with respect to the variation of the echard with different species as well as with different soils. This led to a comprehensive investigation by Hedgcock (1902) of the echard and chresard of some 130 species under control, and 25 in the field. These were largely native and ruderal species, though a number of cultivated ones were included also. The great majority were mesophytes, though they ranged from xerophytic grasses, such as *Bouteloua gracilis*, to such hydrophytes as *Sagittaria* and *Potamogeton*. The author reaches the general conclusion that "the ability of plants to take water from the soil varies in an ascending scale from hydrophytes through mesophytes to xerophytes."

Briggs and Shantz, 1912.—The most complete and thoroughgoing investigation of the echard has been made by Briggs and Shantz in connection with crop-plants for the Great Plains. Their methods and results are perhaps too well known to require comment, but it seems desirable to touch the latter

briefly for the sake of comparison. The term wilting coefficient is employed for non-available water or echard, but it is an exact synonym of these. The determinations of the echard for various soils are in essential accord with those of all other investigators, the values ranging from 1 per cent to 16 per cent, or in the heaviest clays to 30 per cent. But a striking departure from all previous results occurs with respect to the echard for different species. While Heinrich, Gain, Clements, and Hedgcock found differences between species in the same soil represented by a ratio of 1 to 1.5 or 1 to 2, or even more in the case of hydrophytes, the greatest ratio found by Briggs and Shantz was 1 to 1.1. The thoroughness of their work seems to leave little question of the soundness of the conclusion "that the differences exhibited by crop plants in their ability to reduce the moisture content of the soil before wilting occurs are so slight as to be without practical significance in the selection of crops for semi-arid regions." The issue must still be regarded as open with reference to material differences in the echard of native species, and this can only be settled by further research. Recent studies by Dosdall (1919) have shown that *Equisetum* differs greatly from *Helianthus* and *Phaseolus* in its ability to draw water from the soil, as was likewise demonstrated by growing them side by side in the same spots. In seeking to harmonize the discordant results of qualified investigators, it has become more and more probable that types of echard must be recognized.

Water requirement.—In summing up the results of their own researches, as well as those obtained by many earlier observers, Briggs and Shantz (1913: 1:46; 2:88) reach the following conclusions:

Experiments upon the effect of water-content on the water requirement show that the latter increases as a rule when the water-content approaches either extreme.

A reduction in water requirement generally accompanies an increase in the nutrient-content, while a higher water requirement may result from a deficiency in the amount of a particular nutrient.

The type of soil affects the water requirement only though the water or the solutes it contains.

The water requirement increases with the dryness of the air, and is profoundly affected by climatic conditions.

The water requirement varies greatly for different species and varieties. In Colorado, it was found to be approximately 1,000 for alfalfa, 700 for sweet clover, and 300 for millet and sorghum. The grains ranged from 369 for corn to 507 for wheat and 724 for rye.

The greatest value of water requirement work for indicator studies is in connection with the phytometric analysis of climates and habitats. So far as the water relation is concerned, the values obtained by means of phytometers can be expressed in terms of water-loss per unit area or rate of growth, or in the water requirement in terms of dry weight or seed production. For crop plants, the latter are the most important, but for native species all four values must be taken into account, in addition to photosynthetic efficiency.

CONCEPT.

General.—Every plant is an indicator. This is an inevitable conclusion from the fact that each plant is the product of the conditions under which it grows, and is thereby a measure of these conditions. As a consequence, any

response made by a plant furnishes a clue to the factors at work upon it. While this general principle seems to be of universal significance, its application is far from simple. This is because the most direct responses are physiological and for the most part can be determined only by experiment. Such complex physiological processes as growth and reproduction are exceptions inasmuch as they are subject to direct observation. Consequently they are among the most valuable of indicator evidences. Structural responses are the most visible of all, but their exact use is the most difficult since they stand at the end of the process initiated by the causative factors. Structure also possesses a well-known inertia, as a result of which it may register the impact of factors but partially or slightly. Moreover, the adaptation to the habitat may be made in the tissues of the leaf without affecting the gross features to an appreciable degree. A plant may show the most exact response to changing conditions by the behavior of chlorenchyma or stomata, and yet reveal no sign of this in its outward appearance (E. S. Clements, 1905).

The interpretation of indicators is profoundly affected also by the double complex of factors and plants. The species of a community do not always register the same response, nor do they respond to any one factor in the same degree. The habitat itself is still largely a puzzle, and it is often difficult to assign well-marked effects to definite causes. The behavior of individuals, though manifestly of less importance, is not without its difficulties. It is impossible to tell at present whether the varying behavior of individuals of the same species is due to individuality or to minute differences in the habitat. Hence, the problem of indicator values is chiefly one of analyzing the factor-complex, the habitat, and of relating the functional and structural responses of both the plant and community to it. This then makes possible the accurate employment of indicators in practical operations.

Animals as indicators.—Since their response is direct, plants are the best indicators of physical processes and factors. They are by no means unique in this respect. Animals likewise show direct responses to physical conditions and to this extent serve as indicators of them. For a number of reasons they are inferior to plants, however. The chief reason is that their significance is subordinate to that of plants because the latter as food-supply usually constitute the controlling factor. In other words, animals are as a rule indicators of plants more directly than of physical conditions. Their mobility makes the control of a particular habitat or set of conditions less absolute, especially with land animals. With the exception of insects, land animals are much less abundant than plants, and the indications of an animal community are much less complete and definite. Finally, our knowledge of the ecology of animals is much less than that of plants, especially with reference to factor control and succession. In spite of all this, however, animals do have great indicator value, second only to that of plants. While the time has not yet come for an adequate treatment of them in this connection, they are taken into account at various points in the text. Indeed, any other course would be illogical in view of the conviction that the complete response to habitat is the biome, or community of both plants and animals.

Plant and community.—It has already been suggested that the individual, the species, and the community are all involved in the indicator concept.

Each of these has its own value, while all of them must be taken into account sooner or later. Up to the present, the species has almost monopolized the rôle, though the work of Shantz (1911) in particular has emphasized the importance of the community as an indicator. In constructing a complete scale of indicator values, the individual will play a necessary part. Its indications are more minute and subject to greater error. While further quantitative work will increase the accuracy and usefulness of individual indicators, at present they are distinctly secondary. In fact this will probably always be their relative position, inasmuch as they will serve to refine the major indications of species and communities. The question of species and community values is much simpler than appears at first. It is not a matter of employing one to the exclusion of the other, but of taking advantage of their complementary relation. There can be no doubt that the community is a more reliable indicator than any single species of it. This is a necessary consequence of the essential harmony of the important species as to physiological response and factor control. The community not only affords a better norm for the major indications, but it is likewise, so to speak, more finely graduated and hence more sensitive, owing to the fact that no two of its dominants or subdominants are exactly equivalent. It is also a better indicator of the whole habitat, since it levels the variations from one point to another.

The indicator value of a species depends primarily upon its rôle in the community. A secondary or subordinate species may be of little or no practical value, in spite of the general rule. It merely accompanies the major species, or as a subordinate accepts the conditions made by them, thus indicating minor differences. It assumes practical value only in case of the destruction of the dominants, as often happens in overgrazing and in deforestation. Even here the real meaning of a secondary species is due to the fact of its association with more important indicators. The significant species are the dominants and subdominants which give character to definite communities. With these the species and community values approach closely or merge completely. In fact such species give their typical indication only when dominant. Their incidental or scattered occurrences may have meaning, but it is not the normal one. In the present stage of our problem, then, attention should be focussed upon the dominants and subdominants of the climaxes and their various seres. When these have been correlated on the one hand with their efficient factors and on the other with practical processes in agriculture, grazing, and forestry, it will become evident whether an analysis of secondary species is profitable. The dominant may well be regarded as the real basis of indicator study, so commanding is its rôle in the processes of vegetation.

Sequences.—Every indicator owes its value to its position in a cause-and-effect sequence. With this, however, must always be associated correspondence with another cause-and-effect sequence. The value of the compass-plant, *Silphium laciniatum,* as an indicator of corn production rests not merely upon its preference for relatively moist rich soils, but also upon an experiential knowledge at least of the production capacity of such soils. Up to the present, our knowledge of indicators rests chiefly upon the basis of experience. In emphasizing the point that this alone is usually inaccurate and insufficient, there is no intention of failing to give it proper recognition. It is

an essential and often the critical part of indicator research, but its true value can be obtained only by correlation with the other steps of the process. As a consequence, it makes little difference whether the approach has been through experience or investigation. Both must be taken into account before the exact meaning of any indicator is secured. For the future it is clear that much time will be saved by a method of investigation which replaces more or less vague experience by actual investigation.

Direct and indirect sequences.—As is shown later, plants may indicate conditions, processes, or uses. The simplest of these is the first, the most practical is the last. The plant may indicate a particular soil or climate, or some limiting or controlling factor in either. This would seem to be axiomatic, but it is well known that grassland, which is typically a climatic indicator, often occupies extensive areas in forest climates. Thus, the presence of a plant, even when dominant, is only suggestive of its meaning. It is necessary to correlate it with the existing factors and, better still, to check this correlation by experimental planting, or an actual tracing of the successional development.

Indicators of processes usually require a double correlation, namely, that of the plant with the controlling factor, and that of the factor with the causal process, such as erosion, disturbance, fire, etc. Thus, in the Red Desert of Wyoming, roads through the sagebrush are marked by vigorous growths of *Agropyrum.* The latter is here a clear indicator of disturbance. From its usual position in adjacent lowlands, it is presumably an indicator of increased water-content as well. Actual instrumental study alone can determine the exact relation between the disturbance and the water-content, and between the water-content and the presence of *Agropyrum.* The indicator sequence is further complicated by the question whether the increased water-content is due to disturbance directly, to the elimination of competition, or to both. As a matter of fact, however, the field study of *Agropyrum* and *Artemisia* under a wide variety of conditions and in different successional relations indicates that disturbance acts through competition upon water-content.

In the case of use or practice indicators, the sequence differs in accordance with the nature of the crop. When the crop is a natural one as in grazing, the sequence is simple and direct. This is especially true of grazing in which the value of the range is determined directly by actual experiential or experimental grazing tests, which establish the indicator value of each species. With overgrazing, the sequence is similar to that found in process indicators. Trampling disturbs the soil and destroys the less resistant plants. Both effects tend to increase the water-content of the soil and to give the advantage to such plants as *Gutierrezia* and *Artemisia frigida* (Clements, 1897:968; Shantz, 1911:65). This relation is clearly recognizable in the field from the fact that *Gutierrezia,* for example, is characteristic of depressions, alluvial fans, roadways and other disturbed areas. In the case of forests, plants may serve directly as indicators of water or light values, or indirectly of disturbance such as lumbering or fire, and of such practices as reforestation and afforestation. In these processes the crop is partly or wholly artificial, and the indicator sequence is essentially the same as for crop plants. This involves the correlation of indicator and crop plants with their respective habitats, and the close correspondence of the controlling factors in the latter. With forage and

grain crops, the sequence is more complex, partly because the species concerned are not native, but largely because the physical conditions are unnatural as well as controlled. As a consequence, while factor correlation and indicator correspondence are still important, the chief part must be taken by experiment and experience extending over a period of years. It is desirable if not essential that this period be 12 to 15 years, in order to cover the range of conditions from the wet phase to the dry phase of a climatic cycle. This is particularly true in the use of indicators for land classification, in which grazing, forestation, and crop production must all be taken into account.

Direction of indication.—The increasing attention paid to plants as indicators during the past decade has largely arisen from practical considerations. While this is highly desirable, it must be recognized that indicators have also a wide range of scientific application. Moreover, the more important and certain practical values are made possible only through the ecological study of indicators. It is in the ecological sense that every plant is an indicator. The indicators of actual practice will be obtained by the selection of those which are the most distinctive and dependable. Thus, while the indicators for grazing, forestry, agriculture, and land classification will be established by more and more exact study, many indicators will find their chief use in ecology and related fields, which must lay the foundation for the scientific agriculture and forestry of the future.

For these reasons, it is necessary to recognize that every dominant can be used as an indicator of past and future as well as of present conditions. This is due, of course, to the fact that every dominant or subdominant has a definite position in succession. As a consequence, it is an indicator not only of the plants which precede and follow it, but also of the soil conditions in which they grow. At the same time the definite existence of a climatic cycle makes it possible to relate growth and successional movements to climatic changes, both past and future, and to extend the application of indicators correspondingly. On the one hand, this enables us to greatly broaden and definitize the use of plants as indicators of soil, climate, and vegetational movements in the geological past; on the other, it permits us to look ahead and anticipate the changes due to climatic cycles and the development and movements of vegetation and habitat.

Scope.—A complete understanding of the broad significance of indicator studies must rest upon a recognition of the aims and methods of modern ecology. In the early characterization of this field (Clements, 1905:1) it was emphasized that ecology is the central and vital part of botany and that all the questions of botanical science lead sooner or later to the two ultimate facts, plant and habitat. These statements appear even truer to-day in the light of the progress made during the past twelve years. The one essential amplification is the inclusion of zoology, due to the growing conviction that the real unit of response to the habitat is the biological community. Furthermore, it is desirable to place all possible emphasis upon the fact that ecology must fix its attention upon habitat and community in their natural relation. Finally, there must be the clearest recognition of the fact that the plant or animal must be the final arbiter in ecology, except of course in the vast field of human ecology. Fascinating and valuable as they are, instruments and

quadrats are useful only in so far as they tell us what the plant, animal, or community is doing. The most complete records of climate, for example, have no merit in themselves. They acquire value only as the plant or animal discloses by its responses the factors or quantities which are effective or controlling.

The threefold basis of ecology is factor, function, and form (Clements, 1907:1). As a consequence, every ecological fact has its indicator significance, and it becomes possible to determine these just as rapidly as factor correlations are made. The chief objective for the student of indicators is the cause-and-effect relation, and his chief task to show how effects may be used as signs of their causes. In a sense, the use of indicators reverses ecological procedure inasmuch as it leads from effects to causes. Sooner or later it involves a more or less complete system of reading all the evidence afforded by the responses of plants and animals, whether as individuals or communities.

With respect to its application, the scope of indicator work is far-reaching. It not only furnishes a basic method in ecology, and especially in succession, but it is also equally applicable in paleo-ecology. Because it gives us the judgment of the plant upon the physical factors of the habitat, it is indispensable to studies of soil and climate in so far as they have to do with vegetation. For the same reason, it is invaluable in land classification, and to the great plant industries, agriculture, grazing, and forestry. While this is truest of new regions, it holds to some degree for older agricultural communities as well. It applies with especial force to the great unoccupied or poorly utilized interiors of other continents, such as South America, Africa, Asia, and Australia, and is not without meaning for large stretches in Europe. In short, wherever plants grow, in field, forest, grassland, or desert, indicator results are always of some, and usually of paramount, importance.

In their relations to succession and to climatic cycles, plants exhibit some of the most important indicator values. These involve quantitative relations of abundance and growth which in conjunction with factor determinations will give to ecology an accuracy and certainty more and more approaching those of the physical sciences. As a consequence, it will become increasingly possible to definitize ecological processes and principles, and to use them as a basis for accurately forecasting the behavior of plants under changed conditions. Such prophecy is possible at present in any region where an adequate study of succession has been made. Its scope will be extended and its probability increased in just the proportion that instrumental, quadrat, and developmental studies of vegetation become the rule.

Materials.—As has been suggested earlier, while every study of the actual relation between habitat and plant is a possible source of indicator materials, only those are of real value which are based upon instrumental, quadrat, or successional investigations. The permanent foundation of indicator research must be laid by those studies which employ all three methods. For these reasons the published sources of indicator material are relatively few and recent. They are largely American and are confined almost wholly to the period since 1900. In fact, adequate ecological studies having indicator values as their avowed objective are all subsequent to 1910, and are largely due to the appearance of Shantz's paper on the indicator value of natural vegetation in 1911. As a consequence, the present treatise is of necessity based primarily

upon the investigations of the author during the past 20 years and of Shantz for the last decade or more. While these have had indicator plants as a definite objective only since 1908, the preceding 10 years of instrument, quadrat, and succession work were an intrinsic part of the investigation.

Basing studies.—Initial studies of grassland were made in Nebraska from 1893 to 1898. These included a journey along the Missouri and Niobrara Rivers during the summer of 1893, one to the plains and foothills in 1897, and to the Black Hills in 1898. The first ecological expedition to Colorado was made in 1896, at which time a provisional outline of the plant communities was drawn up. Beginning with 1899, all the summers were devoted to investigations in Colorado until 1913, with the exception of that of 1911, which was spent abroad. During the spring and fall from 1899 to 1907, studies in prairies and woodland in eastern Nebraska were carried on with the aid of advanced classes. The six summers from 1913 to 1918, inclusive, have been devoted to vegetation studies throughout the West, with especial emphasis upon succession, indicator plants, and climatic cycles. From 1912 to 1917, the work of the Botanical Survey of Minnesota was directed along similar lines.

The use of quadrats was begun in 1897 and the instrumental analysis of habitats in 1898. The principles of succession were formulated into a working system for the field in 1898 (Clements, 1904:5), while studies of the echard and chresard were first made in 1900. The fundamental importance of the distinction between climax and seral communities was recognized in 1913, and the significance of climatic cycles in 1914. The two most recent advances that extend the use of indicators are the organization of the field of paleo-ecology in connection with the study of Badlands in 1915-16 and the formulation in 1916 of the concept of the biome as the basic biotic unit.

Shantz (1906) began the ecological study of Colorado vegetation in 1903 on the basis of instrumental, quadrat, and successional methods. This led to the direct study of indicator plants on the Great Plains (1911) and in the Great Basin (1914). Out of this grew the extensive series of water requirement studies, as well as of transpiration, made by Briggs and Shantz between 1912 and 1916. During the same period much attention was paid to western vegetation, and this was crystallized in the list of indicator types for land-classification (Shantz and Aldous, 1917) and a map of the climax communities of the United States (Shantz and Zon, 1924). The text accompanying the map contains much information relating to the indicator value of the different vegetation types.

XII. BASES AND CRITERIA.

BASES AND METHODS OF DETERMINATION.

Fundamental relations.—Plants serve as indicators by virtue of their response to conditions about them. Every plant response has some significance, the kind and degree of which must be subjects of exact determination in each case. Some responses are obvious, others less evident, while still others are invisible though demonstrable. All these, however, must be referred to the habitat for the decision as to their meaning and their possible use as indicators. It is clear that the causal relation of the habitat to the plant is the primary basis of plant indicators. Each response is the effect of some factor or factor-complex acting as a cause, and is consequently the indication of this factor. The chief task of the investigator is the measurement of responses, and their correlation with measured factors.

In deciding upon possible bases for an indicator method, physiological responses and physical causes must be given the place of first importance. As further consequences of these must be considered the responses shown in the development and structure of communities, *i. e.*, the basic facts of association and succession. The method of obtaining the facts in these four great fields will continue to be both empirical and experimental. Experiment will steadily increase in amount and value, but the result will be to refine and direct observation and not wholly to displace it. In fact, the more completely experiment is taken into the field, the more readily will observation reveal the meaning of the innumerable natural experiments brought about by changes of habitat and of climate. In this there is no intention of minimizing the crucial value of experimentation, but rather to widen its scope so that all experiments can be taken into account. This is especially important when one recalls the slow advance in experimentation under natural conditions and the insignificant area covered by it. The possibilities of this method have been strikingly shown for many years at the Alpine Laboratory, where numerous examples of natural transplanting in fragmented habitats verify and extend the results of a relatively small number of artificial transplantings. Similar results are to be obtained from natural experiments on a wider scale. The value of *Bouteloua gracilis* as an indicator of climate was graphically shown in the bad-land levels at Glendive, Montana, in 1917. The drying culms of the current year were just half as tall as those of 1916 which still persisted in the same mat. The rainfall for the two years was 26 and 12 inches, respectively. Thus the inevitable adjustment of the short-grass cover to decreased rainfall and water-content furnished results hardly to be surpassed by the most carefully checked experiment.

In indicator work, as in all adequate investigation, by far the best method is that which uses all sources of information and does not emphasize one to the neglect of others. While the very nature of indicators insures proper consideration of habitat and plant, the study of each species must be accompanied by that of its associational and successional relations, and all four of these objectives must be reached by the combined use of observation and

experiment, in which each must be utilized to the fullest capacity consistent with accurate results.

THE PHYSICAL BASIS.

Direct and indirect factors.—An adequate understanding of the habitat as the cause of plant responses that serve as indicators must rest upon two facts. The first of these is that the habitat is a complex, in which each factor acts upon other factors and is in turn acted upon by them. The second is that some of these factors are direct causes of plant response, while others can affect the plant only through them. Water, light, solutes, and soil-air are direct factors of the first importance because of their variation from habitat to habitat. Other direct factors, such as carbon dioxid, oxygen, and gravity, are negligible because of their constancy. Temperature is both direct and indirect, but its indirect action through the water relation is usually the most tangible. Wind, pressure, slope, exposure, soil texture, etc., are all indirect, acting for the most part through water-content or humidity, or through temperature upon these.

Too much importance can not be given this distinction between direct and indirect factors. The indicator value of every plant depends upon it absolutely. A plant can only indicate a direct factor. But by the correlation of the latter with factors which are modifying it, the indicator response of the plant may be related to these. Thus, dwarfed herbs usually indicate a lack of water. In alpine regions this lack is largely caused by excessive transpiration and evaporation due to low pressure. As a consequence, dwarfs are typical indicators of high altitudes and hence of alpine climates. By other correlations of direct factors with causative processes, such as disturbance, erosion, cultivation, etc., plants come likewise to be used as process or practice indicators. The true basis of all plant indicators is to be found in the responses made to direct factors, especially water, light, solutes, and soil-air. These once established, it becomes a simple matter to connect indicators with any correlated factor or process.

Controlling and limiting factors.—It is evident that the factor in immediate control of the behavior of plant or community must be a direct one. But the latter may be profoundly affected by another factor in which the actual control may be said to reside. For example, montane timber-lines are often determined by water, but the availability of the water-content is decided by frost and its sufficiency by the wind. As indicated above, the immediate control and hence the immediate indication must be sought among the few direct factors, while the final control and indication will be found among the indirect factors that exert a critical effect.

All the direct factors of the habitat play a part in the responses of the plant, but only those which vary widely in quantity leave a distinct impress upon it. This is necessarily true, since such constant factors as carbon dioxid, oxygen, and gravity produce fairly uniform responses, and consequently do not differentiate species or communities. In the case of each individual plant or species, its distinctive features are due to one of the variable direct factors. In practically all cases at least one of these will be deficient, with the result that it becomes the limiting factor in the plant's development. This term is used in an ecological sense and not in the physiological one employed by Blackman (1905) and others. As a result the search for indicator correlations among

the four direct factors narrows itself to the one or two which are deficient. Some of these factors regularly bear an inverse relation to each other and all of them often show such a relation. Thus an abundance of water means a lack of oxygen, and a deficit of water a strong soil solution. Habitats deficient in light rarely show a lack of water or nutrients, though the oxygen-content of the soil may be low also. In practically all herbaceous communities, light is usually at the maximum, and the limiting factor must be sought in the soil. Hence, a careful scrutiny of many habitats narrows the search for limiting factors to a single one, and it is then possible to proceed at once with the quantitative correlation of factor and indicator.

It must also be recognized that some factors limit plant response in consequence of an excess. This is true to some extent of solutes and water, but not of light or oxygen in nature. Even with the former, while the excess definitely limits or at least characterizes the plant's activity, the corresponding deficit of water in saline soils and of oxygen in wet ones or in ponds also plays a significant rôle. For water and solutes, it is probably more accurate to say that the extremes, either excess or deficiency, act as limits. While there are statements to the effect that full sunlight is directly injurious to many species, there is little or no conclusive evidence. This feeling has been based largely upon Bonnier's work with alpine dwarfing, which has not been confirmed by similar studies in the Rocky Mountains.

After eliminating the large groups of species that owe their indicator character to the limiting action of water, solutes, oxygen, or shade, there remains a much larger group of sun mesophytes which bear no such distinctive impress. In a mesophytic habitat the four factors are present in a more or less balanced optimum. No one exists in marked deficiency or excess. Yet it has been demonstrated experimentally that a moderate increase in any one of the factors will be reflected in an increase of growth. Each factor in reality exerts a circumscribed limiting action as an outcome of competition between the plants. The various effects, however, are so moderate and so well-balanced that it is practically impossible to separate them. While water is usually paramount and light often the least important factor in the competition between sun mesophytes, all four factors show a limiting action in at least a small degree. In spite of its apparent lack of a distinctive impress, a mesophyte is as much the product of its habitat as the well-marked hydrophyte or halophyte, and serves equally well as an indicator.

Climatic and edaphic factors.—The factors of climate and soil are so intricately interwoven in the habitat as to discourage analysis. For many reasons it is better to ignore such a distinction as of little or no significance to the plant and to fix the attention upon the cause-and-effect relation of one factor to another, quite independently of its location. This will reveal clearly two basic facts, namely, that the habitat is a unit and that the action of this unit is focussed upon plant and community by one or two limiting factors. The relation of the plant to water makes it evident that the distinction is merely one of classification which has no real significance to the plant. Water-content as a direct factor resident in the soil is directly or indirectly the result of precipitation, a climatic factor, and is profoundly affected by humidity, a climatic factor which it also influences. Its availability is determined by soil-texture, solutes, and oxygen, all soil factors, and by temperature, which

belongs to both soil and air, though in origin it is climatic. The baffling nature of the distinction has been well shown by Raunkiaer (p. 6). In one sense, however, the distinction may possess some value. This is with reference to the factors which give character to the great areas marked by climaxes, in contrast to localized ones occupied by successional stages. It is more or less convenient to refer to such areas as climatic or edaphic, if it is recognized that the one denotes a permanent condition over a wide region and the other a relatively transitory stage in a restricted area.

Moreover, the grouping of factors as physical and biotic appears to have little value beyond that of mere classification. Furthermore, it does not conduce to clear thinking to use the same causal terms for the physical conditions which control plants and animals, and for the plants and animals themselves. With the growing recognition of the community as consisting of both plants and animals, the true nature of biotic factors will become evident, and they will be recognized as reactions and coactions.

Climates and habitats.—If one accepts the developmental basis for the study of vegetation, he must also admit the same process in habitats. Habitat and community develop reciprocally from extreme conditions to the final climax controlled by the climate. At this point climate and habitat become merged and are coextensive with the major community, the climax formation. In this connection, however, it is necessary to discard our ordinary ideas of climate and to accept the plant's view of what constitutes a climate. This fact has been appreciated by Wojeikov especially, in his work on the climate of beech (1910). The great grassland climax of North America lends particular emphasis to the difference between climates as determined by plants and by man. In the human sense the climate of southern Saskatchewan is very different from that of northern Arizona, chiefly because of temperature, yet *Bouteloua gracilis* is an important grass in both places and the grassland formation is characteristic of both regions. Likewise the Palouse district of Washington and Idaho with its winter rainfall seems wholly different from the bunch-grass hills of Utah and the prairies of Nebraska; but if the vegetation be taken as the indicator of climate, all three are essentially the same, since they are characterized by prairie associations (Weaver, 1914, 1917).

The acceptance of the climax climate as the major or climax habitat enables us to establish a perfect correlation between habitat and vegetation. The climax habitat will show divisions corresponding to the association, and each association habitat may exhibit subdivisions in agreement with the consociations. This is practically axiomatic, since each community is the product of the factor complex of its habitat. The habitat of one association must necessarily differ from that of another to the degree that one association does from the other. The subordinate communities of a formation, viz., societies and clans, also have their minor habitats, though these are less clearly marked, as would be expected. The structure of the climax climate or habitat corresponds closely if not exactly with that of the climax formation. It may be best illustrated by the grassland climax with its five associations, namely, the true prairie, mixed prairie, bunch-grass prairie, the short-grass plains, and desert plains. While all of these fall in the same climax climate, each one marks a corresponding division of it, or a subclimate. In the case of the true prairie, there are six dominants or consociations, *Stipa spartea, Sporobolus*

asper, S. comata, Agropyrum glaucum, Koeleria cristata, and *Andropogon scoparius,* no two of them exactly equivalent as to habitat. Their requirements approach each other so closely, however, that they occupy the same subclimate, in which they mix or separate in accordance with local variations. An interesting regional separation occurs with the two species of *Stipa,* as well as in the case of *Agropyrum. Stipa spartea* marks the eastern portions of the true prairies and *S. comata* the western; *Agropyrum glaucum* is typically associated with *Stipa comata,* while *A. spicatum* is best developed in the Northwest, especially in the Palouse. The essential point is that each consociation or mixture of two or more marks a subdivision of the association habitat, and is the indicator of it. Similar though minor habitat divisions are indicated by such characteristic societies as those of *Glycyrhiza lepidota, Amorpha canescens, Psoralea argophylla, P. tenuiflora, Petalostemon candidus,* and *P. purpureus,* the water relations of which are essentially in the order given here. In the eastern prairies, where water is abundant, several of these may occur together more or less constantly, but farther west each tends to form a distinct society, and to indicate a corresponding water-content. The differences are slighter than in the case of consociations, and hence society habitats do not necessarily fall in the habitat of a particular consociation. This is probably to be explained partly also by the action of climatic cycles. For example, the wet phase would favor the local extension of *Psoralea argophylla* and *Petalostemon candidus* for a few years, while during the dry phase the less mesophytic *Psoralea tenuiflora* and *Petalostemon purpureus* would have the advantage.

Since the habitat, like the formation, shows development in the course of succession, it exhibits developmental divisions and subdivisions. Each of these necessarily has its own indicator community, namely, the associes, consocies, and socies. The habitats that correspond to these have a time as well as a space relation. If the best-known succession, the hydrosere, be taken as an example, these two relations are shown in the familiar zones of lakes and ponds. Each plant zone or associes from the center of submerged plants to the surrounding climax of forest or prairie indicates a major developmental habitat, *e. g.,* the habitat of the floating aquatics, of the reed-swamp, the sedge-swamp, etc.[1] Each of these associal habitats is subdivided into the habitats of consocies indicated in the reed-swamp, for example, by *Scirpus, Typha,* and *Phragmites,* respectively. Within the latter may be minor habitats characterized by such socies as *Sagittaria, Alisma, Heleocharis,* etc. As a result every region is a complex of climax and developmental habitats of varying rank and extent, each controlling a plant community which serves as the indicator of it.

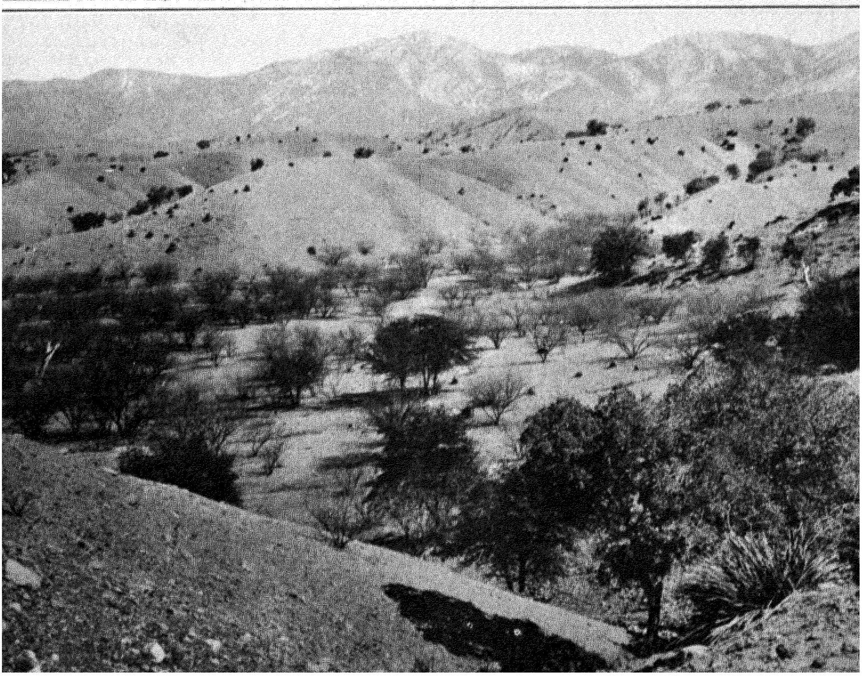
Variation of climate and habitat.—While many reasons make it desirable if not necessary to regard each habitat as a unit, it should be clearly recognized that it varies from place to place and from year to year. The seasonal

[1]Pearsall (1917:78) has recently recognized three associes of submerged plants, namely, (1) linear-leaved associes of *Naias,* etc.; (2) *Potamogeton* associes; (3) *Nitella* associes. This is in full accord with our growing knowledge of vegetational development, which must result in the general acceptance of more rather than fewer units (Clements, 1916: 132). However, the latter must be based upon quantitative studies and checked by extensive scrutiny of other vegetations if the results are not to be mere personal judgments, leading to the condition in which taxonomy finds itself to-day.

variations are more or less of the same character and they are marked by their own indicators in the form of the seasonal societies. A grassland climate is characteristically different from a forest climate by virtue of its product, the grassland climax. This has its explanation in the average difference between the controlling factors of the two during a term of years, but this difference is often less than that shown by the grassland climate in the dry and wet phases of the same climatic cycle. The rainfall of the wet phase if continued for a century or two under natural conditions would turn the prairie into forest, that of the driest period would under the same conditions convert it into desert. Similarly the distribution of rainfall is so erratic that two contiguous localities may show striking differences amounting to the success or failure of a particular crop. Progressive changes of rainfall, temperature, and evaporation occur with increasing altitude, latitude, and longitude. Further, each climate shades imperceptibly into the next, often through wide stretches. These are all elementary facts and the climatologist might well say that they are taken account of in the ordinary way of determining means or normals. As a matter of climatology this is true, but from the standpoint of indicator vegetation it is not. It is a simple matter to trace the line of 20 inches of rainfall, or of the 60 per cent ratio of rainfall to evaporation and to assume that it marks the line between prairies and plains. Such an assumption reverses the proper procedure, in which the associations themselves must be permitted to indicate their respective climates. When this has been done and the limits of the various communities established, it will be possible to determine the correlated factors.

The real importance of climatic variations within a climax habitat lies in the fact that the correlations of vegetation and climate must be studied on the spot year by year. No single station can be typical of the whole habitat, and no year of the whole cycle. Yet for each station and for each year the indicator evidences of the vegetation should correspond closely if not exactly with the controlling factors. As a result, the study of representative localities for each year throughout a climatic cycle should disclose the range of fluctuation in both climax habitat and vegetation, and establish all the indicator values of the latter upon a secure basis.

The minute study of habitats reveals differences which are reflected in the behavior of plant and community, and hence cause the latter to serve as indicators. It is probable that every square foot of a habitat differs in some degree from every other one. Moreover, when the reactions of competing plants are taken into account, the differences are often more minute. In natural studies of competition made in Colorado and in California, as well as in competition cultures, differences of height and flowering have been found for each inch or two. Corresponding differences of density are of even more frequent occurrence in herbaceous communities. These indications have been checked by factor determinations only in a few cases as yet, but there can be little question that many more habitats show the most minute differences, each with the corresponding indication in terms of density, height, reproduction, etc. In short, the indicator correlation of plants and habitats exemplifies a universal principle which applies from the relation between climax formation and habitat through units of diminishing rank to the relation between the individual plant and its miniature habitat.



A. Lowland mesquite (*Prosopis juliflora*) at 2,500 feet in the San Pedro Valley, Arizona.

B. Foothill mesquite meeting oak at 4,500 feet, Patagonia Mountains, Arizona.

Inversion of factors.—One of the early puzzles encountered in indicator studies, especially in connection with succession, was the occurrence of the same dominant in adjacent but diverse areas. This was first noted for *Andropogon scoparius* and *Calamovilfa longifolia* in sandhill and badland regions. These were found in rough areas and in blowouts on the one hand and in meadows on the other. While the seral relations were very different, the relation to water was much the same. On the broken or sandy ridges the soil was porous and the competition relatively small, due largely to the bunch habit, while in the moist meadows the grasses grew in a sod, the competition for water was keen, and the amount for each plant correspondingly limited. A similar inversion in hilly and mountainous regions has since been found for the majority of grass dominants, as well as for an increasing number of shrubs. The breaking-down of the Miocene rim of the Bad Lands of Nebraska and South Dakota yields a talus in which *Rhus, Ribes, Symphoricarpus, Rosa,* and other shrubs occur, all of which form dense thickets in the valley several hundred feet below. *Chrysothamnus, Artemisia,* and *Atriplex* grow far up the walls and buttes of bad lands, and are found again as dominants in the ravines and draws. In the Southwest the desert scrub consists of two major dominants, *Prosopis* and *Larrea.* While they are often mixed in the vast stretch over which they occur, *Prosopis* is typical of the valley and washes. The valley plains and bajadas are characterized by a zone of *Larrea,* above which lie *Aristida-Bouteloua* grasslands wherever broad sloping plains occur. In these *Prosopis* again occurs as a consequence of increasing rainfall, at an elevation of 1,000 to 2,000 feet above its position in the desert (plate 25).

Similar inversions occur in mountain regions, either as a consequence of air-drainage or of exposure, or often indeed of both. In the case of exposure, the general relations are obvious, though the relative importance of water and temperature is usually uncertain. It seems probable that both are directly concerned, and that water plays the primary rôle, except in mountain regions characterized by a very short growing season and minimum night temperatures (*cf.* Shantz, 1906:25; Shreve, 1915:64; Weaver, 1917:44). The effect of temperature inversions was pointed out by Kerner (1876:1) and Beck (1886:3) in Europe and has been studied by MacDougal (1900) and Shreve (1912:110; 1914:197; 1915:82). The latter's conclusions are as follows (1914:115):

"The influence of cold-air drainage might be expected to affect both the upward limitation of lowland species and the downward occurrence of montane species. As a matter of fact the downward limitation of the forest and chaparral vegetation of the desert mountain ranges is due to the operation of the factors of soil and atmospheric aridity, and not to the chimenal factors. The limitation of the upward distribution of desert species appears to be attributable to chimenal factors, as the writer has shown for *Carnegiea gigantea.* The writer has observed that a number of the most conspicuous desert species range to much higher altitudes on ridges and the higher slopes of canyons than they do in the bottoms and lower slopes of canyons. Samples indicate that there is no essential difference between the soil moisture of ridges and the bottoms of canyons during the driest portions of the year. Neither is there any evidence that desert species would fail to survive in the canyon bottoms if they were somewhat higher in soil-moisture content. An explanation of the absence of desert species from canyon bottoms and their occurrence at

higher elevations on ridges must be sought in some operation of the chimenal factors rather than in the factors of soil and atmospheric moisture. An analysis of the operation of the chimenal factors will be sure to discover that cold-air drainage plays an important rôle in determining not only the lowness of the minimum, but also the still more important features of the duration of low temperature conditions."

Measurement of habitats.—The importance of correlating indicator plant or community with the controlling factors of the habitat has already been emphasized. While the standard method of doing this has been by means of physical instruments, a number of attempts have been made to utilize plants themselves for this purpose. While the work of Bonnier (1890:514), in which he made reciprocal plantings of alpine and lowland plants, was essentially of this nature, he seems to have had no thought of using plants as instruments. The first conscious endeavor to do this was perhaps in 1906, when potometers of several different species were used with recording instruments to determine the effect of pressure on transpiration at different altitudes on Pike's Peak (Clements, 1907:287; 1916:439). Sampson and Allen (1909:45) employed sun and shade forms in different habitats at the Alpine Laboratory to determine transpiration in various light intensities, while standardized plants of *Helianthus annuus* were utilized in habitat measurements conducted by the Botanical Survey in Minnesota in 1909. During 1912-1913, Pearson (1914:249) grew seedlings of *Pseudotsuga* beneath aspen and in openings to determine the better habitat for planting operations, and the method has since had a limited application by foresters. The most comprehensive use of the planting method has been made by Hole and Singh (1916:48; cf. Chapter XIII), who established experimental quadrats in the sal forests of India to measure the rôle of shade and aeration in reproduction.

McLean (1917:129; cf. Livingston and McLean, 1916) employed soy beans to measure general climatic conditions by means of growth at two stations in Maryland. The three main criteria used in determining growth were leaf area, stem height, and dry weight of tops, all of which showed the Easton region to be nearly 2.5 times as efficient as the Oakland one. A definite correlation was established for temperature, but not for water, owing to auto-irrigation of the plants. Weaver and Thiel (1917:46) measured the transpiration relation by means of bur-oak seedlings in three habitats, prairie, hazel-scrub, and oak forest, near Minneapolis. Similar measurements were made with maple and elm seedlings in scrub and prairie at Lincoln. Further experiments were made with sun and shade forms of the same species, and with sun and shade branches of the same plant. The species employed were *Acer saccharinum, Ulmus americana, Fraxinus lanceolata, Rosa arkansana, Prunus serotina,* and *Acer negundo.* The general results showed a transpiration 2 to 3 times greater in prairie than in scrub and 6 to 10 times greater than in the *Typha* swamp. Evaporation was regularly greater than transpiration, and no constant relation was found between the two, as would be expected. Sampson (1919:4) has recently made a comprehensive use of *Pisum arvense, Triticum durum,* and *Bromus marginatus* as standard plants in measuring the differences of the climax zones of the Wasatch Mountains in central Utah (cf. Chapter XVI).

The use of plants to measure light intensities has as yet received almost no attention in spite of its great promise. This correlation has been made from the standpoint of adaptation by E. S. Clements (1908:83); when combined with growth and gross form, as in later studies, this method is simple and of great value. Even more significant is the use of standard plants for measuring light intensity and quality by means of the photosynthate produced in unit areas. Preliminary work of this nature has been carried out by Clements and Long (Clements, 1918:29; 1919; cf. Long, 1919) in the habitats at the Alpine Laboratory, and the chemical procedure has been refined to furnish a basic method of general application. The use of plants as instruments for habitat analysis is further discussed on a later page.

THE PHYSIOLOGICAL BASIS.

Kinds of response.—With rare exceptions a physical factor produces a functional response. Such responses are the most direct and the most accurate measures of the habitat, and hence would serve as nearly perfect indicators were it not for their being invisible. Fortunately, functional responses when marked regularly bring about structural changes which are visible. This is especially true of growth which, as the middleman between function and form, has the advantage of being direct as well as visible. Growth, like structure, has the further merit of showing qualitative as well as quantitative differences and thus serves as an obvious record of abnormal response. From the standpoint of indicators, it is desirable to take all three kinds of response —function, growth, and structure—into account and to assign to each its proper value. The relative value is indicated by the sequence of the three as successive effects of controlling factors as causes. The rapidity and accuracy of the response decreases with the distance from the impinging factors, while the readiness of its recognition correspondingly increases. As a consequence, indicator values have so far been based largely upon species and form. The importance of growth has later been recognized and it is but recently that function has been taken into account. In the further investigation of plants as habitat measures and indicators, it is essential to determine the functional responses first, as the most direct and quantitative. These should then be correlated with growth measures and the latter with structural adaptations. When this has once been done, either structure or growth can be used as ready and accurate measures, without resorting each time to the experimental analysis involved in functional measurements. As a matter of practical application, however, it is probable that growth and reproduction will serve as the best indicators of conditions for crop plants since the habitat is more or less controlled. In the case of forest and grassland, where the factors are essentially natural, a further analysis by means of functional determinations seeems desirable if not imperative.

Effect of habit.—There are three reasons for the superiority of function over form for indicator correlations. The first is that considerable adjustments to factors can occur without affecting structure at all, the demands being fully met by functional responses. Another is that there is almost always a lag between function and structure, by which the effects of a factor appear in the latter only after a time or in diminished degree. These reasons are relatively unimportant compared with the rôle of habit, however, and the

second is perhaps only a consequence of the latter. While there has been little experimental study of habit as such, there are many suggestions of its importance in modifying or reducing response, especially in structure. This influence of habit is well known to foresters and agriculturists in connection with the germination of seeds from different regions and the behavior of their seedlings. It has also been shown in the case of alpine species transplanted to lower levels in that some retain the dwarf habit and others do not (Bonnier, 1890), and for subalpine trees, some of which change their form and not their seasonal phenomena, while others reverse this behavior (Engler, 1912:3). The response of herbaceous species grown in two or more habitats is equally significant. Some are so responsive or plastic that both form and structure show practically perfect adjustment to each habitat in the first generation. Others modify the form and not the anatomy, and still others the interior of the leaf but not its form. There are all degrees of completeness of response to the stable plant, in which form and structure change little, and all the adjustment must be secured through function (E. S. Clements, 1905:93).

As a consequence, the indicator value of any species can not be known until its functional response has been measured and correlated with the structural. This does not mean that the constant occurrence of a species in certain conditions can not be turned to practical account, but it does suggest the wisdom of regarding such correlation as tentative until the functional indication has been determined. The latter will also solve the puzzles presented by communities in which very different life-forms, such as evergreen and deciduous trees, appear to flourish on equal terms. The most striking case of the masking of the real response by habit is seen in such leafless rush-forms as *Scirpus lacustris* and *Equisetum,* in which it is now proved that the functional response is that of a hydrophyte (Sampson and Allen, 1909:49; Dosdall, 1919).

Individuality in response.—Indicator values center about the species. Uniformity of behavior under uniform conditions and clear-cut adjustment when these are changed are the essentials of a good indicator. For these reasons it is important to deal chiefly with species which are represented by many individuals, such as dominants and subdominants, and hence to use the community as the basis for indicators. This makes it necessary to determine the range of individual response in function and growth as well as in structure. In developing the use of standard plants as instruments, this matter is of the first importance. While the question of standardization will always enter, it will be convenient to use those species in which the individuality of functional response is slight. In the use of indicators, the range of individual behavior is a less important consideration than the knowledge of the range.

Sampson and Allen (1909:37) have studied the individual behavior of four montane species as to transpiration and reached the following conclusion:

"Only slight variations occur, not usually exceeding 3 mg. per square centimeter for a period of 12 hours. Therefore, it may be concluded that plants of the same species grown in the same habitat when tested under the same physical conditions show but slight variation in transpiration per unit of surface exposed."

Effect of extreme conditions.—The significance of extreme conditions for response and the relation to indicator values is shown by the case of xerophytes and halophytes. While the latter are now known to be merely

xerophytes of a somewhat special type, they were long thought to constitute a distinct class. This is still true in a measure of those species which tolerate salts directly injurious, but it is well known that the majority owe their impress to physiological dryness due to the abundance of salts. But, while halophytes are indicators of arid conditions, it is a special type of aridity, and the indication must not be assumed to mean just what it does in ordinary soils.

A somewhat similar case is afforded by the evergreen shurbs. In spite of the work of Kihlmann (1890:88, 105), it has been generally assumed that the evergreen shrubs of bogs, such as *Chamaedaphne, Andromeda, Vaccinium, Ledum,* etc., were xerophytes essentially similar in water relations to evergreen shrubs of arid climates. Recently the experiments of Gates (1914:445) have confirmed the conclusions of Kihlmann that while they are xerophytic, it is in response to physiological dryness in winter, and that they do not indicate aridity in such habitats during the summer. In fact, the summer indications are rather those of deficient aeration.

When growth is considered, the response of the same species to different extremes of one factor or another is often very similar. E. S. Clements (1905:93) has found in control experiments with *Chamaenerium, Aquilegia,* and *Anemone* that extremes of any factor which are not optimum for the species tend to dwarf plants growing in them. The general principle has been formulated as follows by Clements (1905:105):

"When a stimulus approaches either the maximum or minimum for the species concerned response becomes abnormal. The resulting modifications approach each other and in some respects at least become similar. Such effects are found chiefly in growth, but they occur to some degree in structure also. It is imperative that they be recognized in nature as well as in field and control experiment, since they directly affect the ratio between response and stimulus."

This applies with especial force to the recognition of indicators, since their value depends primarily upon the close correspondence between response and the causative factor.

Phytometers.—The best indicator of the nature of a habitat and of its practical utilization is the particular plant or community concerned. This is axiomatic, but it needs emphasis in connection with the experimental study of indicators. Such study may be made by means of physical instruments, standard plants, or the plants to be grown as a natural or artificial crop. The former is the simplest of the three, the latter the most effective. The use of standard plants combines the advantages of both to a large degree, and seems destined to undergo extensive development during the next few years. The refinement of method will lead to an increasingly wider range of possible standard plants, until it includes a large number of the species of greatest importance in agriculture, forestry, and grazing. Out of these will emerge a few species of broad powers of adjustment and adaptation which can be used as measures over great areas, such as between the associations of a climax formation or even between climax habitats themselves. A number of species of this sort are already clearly pointed out by their vast ranges and their vigorous growth in different regions. Of the grasses, *Bouteloua gracilis, B. racemosa, Stipa comata,* and *Andropogon scoparius* are perhaps the most

promising, and among shrubs *Rhus trilobata, Cercocarpus parvifolius, Ceanothus velutinus,* and *Rubus strigosus.* Of the trees, aspen is the best, with *Pinus ponderosa* and *Pseudotsuga mucronata* as the best of the conifers for the western half of the continent. As general standards, such weedy herbs as *Helianthus annuus, Melilotus alba,* and *Brassica nigra* are most useful. The most satisfactory cultivated plants are yet to be determined, but wheat, corn, and beans have obvious advantages.

Preliminary results justify the feeling that standard plants or phytometers can be developed with more or less readiness to measure varying amounts of the direct factors, water, light, temperature, soil-air, and solutes. Such functional responses as transpiration and photosynthesis furnish the most accurate measurements, but growth responses are also of the greatest value, especially where factor-complexes are to be measured. Determinations based upon responses in form and structure are also distinctly valuable. Because of the longer time involved, they do not permit of such complete control, and their correlation is less exact. In all of these, the error due to individual behavior must be checked out by careful selection of individuals and by using a number sufficiently large to yield a mode and to permit the elimination of those which depart widely. In addition it has proved increasingly desirable to use a battery of two or more species as phytometers, since this increases the number and accuracy of the results quite out of proportion to the extra labor involved.

The first application of the phytometer method was made by Clements and Weaver (Clements, 1918:288; 1919) at Pike's Peak in 1918 and 1919. The plants used were sunflower, beans, oats, wheat, sweet clover, and raspberry, *Rubus strigosus.* These were grown in sealed containers, with plants in open pots as checks on the conditions for favorable growth in the former. The normal number of pots for each species was 3 to 5, but this was often reduced by mishaps. Three series were grown during the summer, the period varying from 28 to 45 days. The habitats measured were those of the short-grass associes at 6,000 feet, the half-gravel associes, the gravel-slide associes, and the *Pseudotsuga* consociation at 8,500 feet, and the *Picea engelmanni* consociation at 9,000 feet. Stations were visited each week for the purpose of making weighings and of reading the various recording instruments. The responses primarily considered were transpiration and growth, though photosynthesis was measured also. These showed marked differences with reference to altitude, degree of shade, and seasonal factors. The relative values were the same for the native *Rubus* as for the cultivated plants, and the complete results seem to leave no question of the paramount importance of plants for the quantitative study of habitats and communities (cf. Clements and Goldsmith, 1924).

The use of several dominants in a phytometer battery amounts almost to employing a plant community as a measure, and suggests the possibility of utilizing portions of actual communities in this way. The simplest way of doing this at present is by means of permanent quadrats which are visited each month or each year and growth actually recorded by height or volume measures or by weight. Since many communities containing both dominants and subdominants, such as *Stipa* with *Amorpha canescens, Psoralea tenuiflora,* and *Brauneria pallida,* occur throughout the area of most climaxes, a

series of quadrats containing essentially the same population can be established through a wide range of conditions. Locally, where diverse habitats are found within short distances, as in the case of zones about ponds and of dynamic areas, it is not difficult to transfer soil-blocks of the same community to several different habitats and to follow their behavior in terms of the growth and abundance of the species concerned. Such communities afford the best possible measure of the seral habitats and reactions typical of succession, especially when reciprocal transfers are made between two contiguous or successive stages (Clements and Weaver, 1924).

THE ASSOCIATIONAL BASIS.

Nature of association.—The association of two or more species in a community is due to one or two of the following three reasons: (1) general similarity of functional response to controlling factors; (2) dependence upon the reactions of the dominants modifying these factors; (3) dependence upon the autophytes as hosts or matrices. The last two reasons also explain as a rule the presence of the animals of a community as well. Hence it is obvious why one species of a community should indicate the actual or probable presence of the others regularly associated with it, and likewise the corresponding factors. This principle is susceptible of extended application, but it is nowhere more striking than in the case of relict herbs of a former forest. Though axiomatic, it must be used with some care, since no two species are exactly alike in response and indication, and since successional factors often enter to cause confusion.

The occurrence of a dominant indicates not only the presence or possibility of its associated dominants, but also that of the related subdominants, secondary species, hysterophytes, and animals. This is as axiomatic as it is patent in the case of an actual community in the field. This relation becomes of real indicator significance where the community is partially or largely destroyed, when it is rapidly changing, or is but incompletely known, especially in the case of fossil vegetation. A subordinate species likewise indicates other subordinate species as well as the controlling dominants, except in those plants which occur in two or more associations or formations, as well as in different seral stages. Even hysterophytes have a distinct indicator value when they are restricted to particular hosts. Moreover, it is clear that the associational relation signifies that animals may often be indicators of plants, as well as plants of animals.

Dominants.—A dominant is the most important of all indicators. This is due to several reasons. The first of these is that it receives the full impact of the habitat, usually throughout the growing period. The second reason is that it reacts upon the controlling factors, and thus modifies the response of its associates. It also marks the progress of succession and consequently is bound up in a sequence of dominants, with the result that it affords both developmental as well as associational indications. In addition, it shows great abundance over extensive areas and occupies a wide range. In fact, its very dominance is the sign of its success under the conditions where it controls. However, it is necessary to recognize that a dominant species is not always dominant, and that its control may be local and developmental in parts of its range, while it is extensive and climax in the main portion.

Bouteloua gracilis is one of the most exclusive of climax dominants in its typical area, the short-grass community of the Great Plains, but it becomes a co-dominant or merely a successional one in the related associations of the grassland formation, and on the edge of adjacent climaxes, such as the chaparral and the sagebrush. In the *Stipa-Sporobolus* prairies it is subclimax on the ridges and drier slopes, while in the *Aristida-Bouteloua* desert plains it is usually subclimax also, but in the valley plains and swales it is truly climax. In all three associations it possesses indicator value as a dominant, but this value is different in each one, both as to its associates and the relative conditions. Near the edge of its range it loses its dominance and becomes merely a subordinate member of the community with a greatly modified or restricted significance.

The distinction between the dominance and the mere presence of a species is vital, from the standpoint of the structure of vegetation as well as from that of indicators. It is this which makes catalogues, lists of species, and general descriptions of the flora of a region of little value to the ecologist. In fact, such materials are trustworthy only in associations already known, where they are superseded. This is exemplified by a number of grass dominants. *Bouteloua gracilis* is found from Manitoba to Wisconsin and Mississippi, west to Texas, central Mexico, and California, and northward to Alberta and Saskatchewan. It occurs as the characteristic climax dominant of the short-grass community only in eastern Colorado, southwestern Nebraska, western Kansas and Oklahoma, northeastern Arizona, northern and eastern New Mexico, and in the Panhandle and Staked Plains of Texas. Usually with *Bulbilis*, it is more or less regularly associated with *Stipa* and *Agropyrum* from northwestern Nebraska and northern Wyoming through the Dakotas and Montana, into Saskatchewan. Altogether it is a climax dominant over perhaps a quarter of its range and a seral dominant over another quarter. *Stipa comata* is a climax dominant to-day only in Nebraska, northern Colorado, Wyoming, the Dakotas, Montana, and Saskatchewan, though it ranges from the latter to Nebraska, New Mexico, California, and northward to Alaska. As a consequence, the vegetational and indicator importance of any dominant species can be determined only by field studies of its abundance and rôle. Maps and conclusions based upon the distributional area alone are both misleading and erroneous.

Equivalence of dominants.—The dominants of a formation owe their association to the generally similar responses which they make to the climax habitat. This fact is further attested by the identity of life-forms and, to a small degree as yet, by actual measurement of the controlling factor. As the sum of similar responses, the formation is thus the largest and most distinctive of all indicator communities. Within the formation the dominants fall into associations by virtue of still closer similarity in response. Thus *Stipa*, *Sporobolus*, *Agropyrum*, and *Koeleria* constitute the climax prairies. By their height and general turf habit they indicate a rainfall of 20 to 30 inches. *Bouteloua gracilis* and *Bulbilis dactyloides* form the short-grass plains. Their short stature and mat habit are responsive to a smaller rainfall of 12 to 22 inches, which in effect is much reduced by evaporation. The *Aristidas* and *Boutelouas* of the desert plains from Arizona to western Texas are somewhat taller, but their bunch habit is an index of a smaller water efficiency, largely the

result of excessive evaporation. This relation is further indicated by the presence of *Bouteloua gracilis* in the moister valleys, and by the fact that *Stipa* and *Agropyrum* regularly mix with the short-grasses as indicated above, but have never yet been found mixed with the species of *Aristida* and *Bouteloua* characteristic of the desert plains. So far as our present knowledge goes, dominants of the same association or of the same associes are never exactly equivalent. Actually, they may seem to be since the annual variations of the climatic cycle are often much greater than the difference in conditions. Even here, however, they tend to maintain their position or abundance, relative to the controlling factor. As a consequence, each consociation has its own indicator value, which, so far as its presence is concerned, necessarily varies somewhat from wet to dry phases of the cycle, but is checked by corresponding variations in growth, reproduction, and abundance. Thus, *Stipa spartea* and *Agropyrum glaucum* show climatic differences from *S. comata* and *A. spicatum*, while *Stipa comata* and *Agropyrum glaucum* occur together over thousands of square miles, but are differentiated by water relations determined by soil and slope. The actual physical differences in equivalence are slight, and hence the dominants of an association tend to mix or to alternate intimately instead of being pure over wide areas. However, this is necessarily truer of an association with several to many dominants than of one with but a few (cf. Zon, 1914:124).

Each dominant will grow in a fairly wide range of conditions, but will thrive only in a much narrower range. The field optimum for each is not a single point but an area. The areas of the dominants of the same association or associes overlap to such an extent that they coincide except at the extremes. If the ranges of normal adjustment of *Stipa comata* and *Agropyrum glaucum* be represented in each case by a rectangle, the two rectangles will coincide for three-fourths of their lengths approximately. This indicates the degree of equivalence, the projections of each rectangle representing the actual difference in water-response for each species. This overlapping has its real counterpart in communities where the dominants are zoned. The mixed area between two zones represents the range of factors for which the two dominants are equivalent, and the pure zone on either side indicates the range peculiar to each. There is no necessary correspondence between the width of the zones and the mixed area, and the range of factor coincidence for the two dominants, owing to the varying rate at which such a factor as depth of water or amount of water-content may change. In the lakes of Nebraska, the two successive dominants, *Scirpus* and *Typha*, occupy the same depths from a few inches to several feet. Over most of this range they are mixed or alternating, but beyond 4 to 5 feet *Typha* drops out, while *Scirpus* may persist to a depth of 6 to 7 feet. Except where shores slope rapidly, the mixed zone is many times wider than the zone of pure *Scirpus*.

In this connection it should be recognized that dominants show a wider margin between the normal range and better conditions than between it and worse conditions. In other words, a species is quickly and definitely limited by unfavorable factors, while those generally favorable to growth exert little limiting effect, the real effect being due to competition. This is the obvious explanation of the number of dominants and the abundance of species in sunny well-watered habitats, such as prairies, open woods, alpine meadows,

etc., and their paucity in deserts and saline wastes. In short, abundance is itself an indicator, whether it concerns the individuals of one species or the species of a community.

Absence of dominants.—The absence of a dominant from its particular community is often of indicator significance. A dominant may be lacking as a result of several different causes. Its absence may be due to unfavorable controlling factors, to very uniform conditions, to competition, destruction, or to the failure of invasion for any reason. In all of these cases except the last, absence has a definite indicator value, though it is practically always supplementary to the presence of its associates. This is perhaps its chief value, in that it enables us to check the positive indications obtained from presence. Absence due to unfavorable conditions or to competition is the rule. Uniformity of conditions, however, is a more frequent cause than has generally been recognized. This is well illustrated by shallow lakes in the sandhills of Nebraska, where the depth is so uniform that *Scirpus* is the sole dominant in spite of the fact that neighboring lakes show *Typha, Zizania,* and *Phragmites.* Absence as a result of destruction is usually difficult to determine and yet is of the greatest indicator importance. The grassy parks of the Uncompahgre Plateau in Colorado are so extensive and appear so permanent that their real significance, as well as that of the absence of the trees, was finally determined only by the discovery of burned wood deep in the soil. Similarly, much evidence has been found to show that the absence of *Stipa* or *Agropyrum* over wide stretches of the Great Plains reveals overgrazing of a type that has never been suspected. Thus, while absence is necessarily correlated with the presence of the related dominants in order to be usable, it does furnish indications of much value.

Subdominants.—Subdominants are species which exert a minor control within the area controlled by one or more of the dominants of an association or associes. They are the successful competitors among the species which accept the conditions imposed by the dominants. As a rule they differ from the latter in life-form, and their competition is largely mutual rather than with the dominants. This is obviously the case in forests where the subdominants form layers. In grassland, where light controls in a minor degree alone, the layering is in the soil, but with a somewhat similar result that the dominants use the water before it reaches the deep-rooted herbs. In prairie and meadow, there is often enough water for both, a condition favored by the fact that subdominants reach their maximum at different times during the season, and hence cause the characteristic seasonal aspects. During dry phases of the climatic cycle, however, there is direct competition between dominants and subdominants, but usually at the expense of the latter.

Within the limitations set by the dominants, subdominants follow the same general principles as to indicator values. This applies to their association in a community, either climax or seral, their equivalence, their dominance as compared with mere presence, and to their absence. They diverge, however, in exhibiting a seasonal sequence in many associations, by which they appear to escape too intense competition with each other. Prairies purple with *Astragalus crassicarpus* in April and May are covered with *Amorpha, Psoralea, Petalostemon* and *Erigeron* in June and July, and these in turn yield to golden rods, asters, and blazing stars in August and September. To

A. *Pentstemon gracilis* as a climax subdominant in mixed prairie, Gordon, Nebraska.
B. *Pedicularis crenulata* as a seral subdominant in a *Juncus-Carex* swamp, Laramie, Wyoming.

a large extent these successive societies occupy the same ground and would seriously compete with each other were it not for the fact that the maximum demands of *Astragalus,* for example, are over before those of *Psoralea* and *Erigeron* begin. Societies thus have a time as well as a space value as indicators. While the subdominants of the same aspect are equivalent to a large degree, those of the three aspects, spring, summer, and autumn, differ in being progressively more xerophytic, owing to the seasonal relations of rainfall and evaporation. Societies are not only most numerous and best-developed during the early summer because of optimum conditions, but they likewise reach a maximum in those communities with optimum conditions, such as prairie and forest. In the short-grass plains they are greatly reduced, and in desert they are relatively few, except in the spring. This exception covers those deserts with two rainy seasons in which the socies of winter and summer annuals are possible only because of a relative excess of moisture near the surface at these times (plate 26).

Secondary species.—This is here used as an inclusive term to comprise all the autonomous species of a community outside of dominants and subdominants. Their subordinate importance has caused them to receive relatively little attention, but their correlation with habitat factors has gone far enough to show that they all possess indicator value to some degree. In a sense, this is thrice removed from the habitat, since in climax communities in particular the conditions to which secondary species respond have been modified by the dominants and then by the subdominants. Secondary species either make minor communities such as clans, *e. g., Antennaria dioeca, Meriolix serrulata, Anemone caroliniana, Delphinium carolinianum,* etc., or they occur as scattered individuals in society or consociation. When they form more or less extensive clans which recur throughout an association, their indicator value approximates that of a subdominant. In fact, it must be recognized that some of the most important clans might well be regarded as societies. Or to put it more clearly, some subdominants vary sufficiently in abundance and control from place to place and year to year that they may form societies at one place or time, and clans at another. Apart from these, clans and scattered species have their chief importance in revealing minor differences of habitat within the consociation or society. They are often due to small disturbances and to succession in minute areas, and derive their indicator significance from this fact. It is probable that the careful study of secondary species will disclose some indicators of much sensitiveness and usefulness.

Plant and animal association.—It is desirable for many reasons to consider animals an intrinsic part of the community as a biological unit. The great value of this is that it insures an adequate and correlated treatment of both plants and animals. It does not change in the least the basic relations between physical factors, plants, and animals, upon which their mutual indicator significance depends. Just as the plant indicates the factors and processes to which it responds, so does the animal serve as an indicator of the plant or community which furnishes it food, shelter, or building materials. The animal also indicates physical factors in so far as they affect it directly. The plant, however, has a double indicator relation by virtue of its response to factors on the one hand and of its control of animals on the other. Since

animals are mobile for the most part, the control and the indications afforded by plants are necessarily less definite and exact. While the study of animal communities has gone far enough to provide a qualitative basis for plants and animals as reciprocal indicators, there has been no conscious endeavor to investigate this relation as yet. This is not true of paleontology, however, in which such causal relations as that between grassland and grazing animals have long been used. Even here an adequate and comprehensive system must await a fuller development of indicator values in present-day communities. A preliminary attempt at such a system in both ecology and paleoecology is made in Chapter XIII.

THE SUCCESSIONAL BASIS.

Scope.—Since the nature of the habitat and the character of the population are constantly changing in all seral areas, succession is of profound importance in connection with indicators. While the basic rule that plants respond to the controlling factors holds for developmental as well as climax communities, the indicators change as the succession advances. Each stage of the succession is marked by factors that act upon species, which react in turn. Hence the indicator relations change more or less slowly but inevitably from one stage to the next. While the developmental areas of a formation are very much less in aggregate extent than those occupied by the climax stage, they are so numerous and various as to demand constant attention. The relative permanence of an indicator relation depends wholly upon whether it is determined by developmental or climax conditions. Since the use of any area for cropping, forestation, or grazing either demands or effects constant changes in it, succession is the basis of all utilization of communities or dominants as indicators. This is especially true in the case of land classification, as Shantz has shown (1911:18), and it applies also to all engineering and construction operations in which the soil is disturbed or new habitats produced.

Sequence of indicators.—Succession has been defined and analyzed as the development of a complex organism, the climax community or formation (Clements, 1905:199; 1916:3). It is a chain of causally related functions or processes. Development begins at certain definite points, pursues a regular course, and ends in the final or mature stage, the climax. As a result, each seral dominant or community has indicator values beyond those arising from the basic relation between plant and habitat. Each stage is the outcome of those that precede and the precursor of those that follow until the climax is reached. It indicates not merely the existing conditions, but it also points backward through successively remote stages to the beginning of the sere, and forward through those which lead up to the climax. Since the development of the habitat proceeds step by step with that of the formation, each stage is an indicator of earlier and later habitats as well as communities. Succession, moreover, is always progressive, and makes it possible to forecast not only the direction of development but something of the rate as well. It depends primarily upon the production of new, denuded, or disturbed habitats, and thus serves as an indicator of the many processes, physiographic, biotic, etc., which initiate new habitats or denude existing ones.

The several indicator values of a seral community depend primarily upon the climax and the sere to which it belongs. The climax determines the domi-

nants and subdominants from which the stages are drawn, indicates the climate in general control of the habitat changes, and constitutes the final stage toward which all the successions are moving. It is in itself an indicator of succession, since it permits the prediction of the general course of development that results from any disturbance in it. The division of seres into primary and secondary rests upon the double basis of habitat and development, and explains why each sere has indicator significance in itself. The primary sere or prisere indicates an extreme condition of origin, such as water or rock, slow reaction on the part of the earlier communities especially, and hence a large number of successive communities. The secondary sere or subsere begins on actual soil in which the conditions are not extreme, requires less reaction, exhibits few stages as a rule and runs its course to the climax with much rapidity. All seres, but primary ones in particular, are distinguished upon the basis of the climax and the water relations of the initial area. The great majority of seres are mesotropic, that is, they progress to a mesophytic climax. In desert regions they are xerotropic and in the tropics may be hydrotropic (Whitford, 1906). Their indicator meaning varies accordingly, but it is even more subject to the water-content of the initial area. Seres are termed hydrarch (Cooper, 1912: 198) when they originate in water or wet areas, and xerarch when the initial condition is xerophytic or at least considerably drier than the climax. The nature and indicator value of hydroseres differ in accordance with their origin in lakes and swamps, or in bogs or other poorly aerated wet soils (oxyseres). Similarly, the indicator values of xeroseres vary with their origin upon rock, dune-sand, or in saline areas.

Major successions as indicators.—The seres or unit successions discussed above are themselves parts or stages of greater successions. The cosere is a series of two or more unit successions in the same spot, and is best illustrated by those peat bogs in which the remains of the various stages and seres are accumulated in sequence and in position. In addition to the indications furnished by each sere, the cosere always indicates one or more striking changes of condition. When it exists over a wide area or recurs in the same relation in several regions, it is an indicator of climatic change. An effective change of climate is denoted by the occurrence of the peat formed by water-plants as the layer above that which records the presence of the climax or subclimax trees. Such coseres have been industriously studied by European investigators, Steenstrup, Blytt, Sernander, Lewis, and others (Plant Succession, 378) and their climatic correlations established with much certainty. The record of a cosere is well preserved in water and especially in peat-bogs, but the more or less fragmentary records furnished by burns, dunes, moraines, and volcanic deposits are often of great value. This is especially true of the deposits of periods of great volcanic activity, such as the Miocene, as found in Yellowstone Park and the John Day Basin (Plant Succession, 367).

Major changes of climate are accompanied by the shifting of climaxes as well as by the succession of seres in the same spot. The differentiation of climates during the Paleophytic and Mesophytic eras led to corresponding differentiation of vegetation with characteristic zones grouped around centers of deficiency or excess. These zones were clearly marked out by the opening of the Cenophytic era, since which time the major effects of climate have

been recorded in their shifting. It seems highly probable that the climatic cycles which produced and characterized the glacial period were accompanied by marked shifting of climax zones and that the close of the period left the primary zones of continents and mountains much as they are to-day. Such zones are the most striking and important of all climatic indicators, and their significance has been appreciated and investigated for more than a century. Perhaps even more important is the fact that such a series of shiftings or zones is a successional process by which it becomes possible to predict the general effect of any climatic cycle. This relation has already been developed to some extent (Plant Succession, 347, 364) and is further discussed in connection with paleo-ecology (Chapter XIII). The greatest climatic changes of geological times are thought to be indicated by the evolution of the great land-floras and their differentiation into climax vegetations. Thus, the entire course of the development of the earth's vegetation, which is called the geosere, is divided into eoseres corresponding to the three great eras, and each eosere then exhibits clisere shifting in response to lesser cycles. The use of zones as indicator criteria is discussed in the next section.

THE EXPERIMENTAL BASIS.

Nature.—Indicators derive their importance chiefly from their practical applications. For all practical purposes, indicator values must finally be determined by experiment. The degree of their usefulness will depend mostly upon the kind and thoroughness of the experimental test. The planting of a trial crop by a settler will give some idea of the indicator meaning of the native vegetation that has been removed. In such a case the evidence is slight and its value tentative. If the planting is repeated for several years or is extended to other farms or localities, its value increases accordingly. As this is the usual course for a crop in a new region, it is obvious that ordinary agricultural practice must suggest indicator correlations with crop plants. This is well known to be the case, but the actual utilization of indicators by farmers seems always to have been inconsiderable. This is largely due to a lack of knowledge of native plants, especially in a new region, but also to the fact that this knowledge was needed most in selecting land and choosing crops, at a time when it was still to be acquired. Thus, while the aggregate experience of a neighborhood might possess real value, there has rarely been any method of formulating it and making it effective.

The extension of experiment stations and substations throughout the West initiated the period of scientific study of agricultural problems. The investigations were directed chiefly to the selection of the best varieties for different regions and soils and to the improvement of yields. Unfortunately, the botanist was not interested in the problems of field crops and the agronomist was little or not at all concerned with native vegetation. The result was that a great mass of experimental data remained unavailable because it lacked correlation. It was possible to give this only through ecological studies, and then only after quantitative methods had been devised for the analysis of habitat and community. As a consequence, exact and purposeful studies on indicators date from the present decade for each of the three great fields, agriculture (Shantz, 1911), forestry (Clements, 1910), and grazing (Clements, 1916: 102; 1917: 303; 1918: 296; 1919). In spite of this late beginning, the recog-

nition and utilization of indicators are destined to undergo rapid development. This is especially true of forestry and grazing, owing to the fact that the corresponding experiment stations and reserves are organized upon the basis of exact ecology.

Essentials.—It has already been insisted that experiment affords the only decisive test of an indicator. A single experiment may do this if properly checked, but repetition is regularly necessary to cover the range of conditions in space and in time. The experiment itself must be made with the fullest knowledge of the factors concerned as well as the vegetation to be correlated. As already pointed out, this involves quadrat study of the community and its successional relations, and instrumental study of the habitat and its variation through the climatic cycle. The thoroughgoing application of this method makes it possible to take advantage of countless natural happenings to convert them into experiments. The number of such possibilities furnished by denudation, lumbering, fire, cultivation, grazing, etc., is countless. If adequately utilized, they will not only greatly reduce the number of set experiments necessary, but will also make the latter possible on a scale otherwise out of the question. The natural experiment has the advantage in economy of time and effort, and in repetition of examples. The checked experiment permits of a definite choice as to time and place, and allows greater control. It is the essential task of experimental ecology to combine these into a complete method, which will give quantitative results throughout the field of ecology as well as in connection with indicators. This is one of the primary objects of the present treatment, though the indicator relations are necessarily given first place.

INDICATOR CRITERIA.

Nature and kinds of criteria.—Every response of the plant or community furnishes criteria for its use as an indicator. These are most serviceable when they are visible, but demonstrable functional responses may be even more valuable, though invisible. The evidence as to functional responses in natural habitats is still very limited, and will be considered in the next chapter under the factors concerned. Here the discussion is confined chiefly to the criteria afforded by form and structure, with which growth is included. The development of the community is also considered along with its structure for the same obvious reasons.

Criteria may first be divided into two kinds in accordance with their relation to the individual plant or to the plant community. Individual criteria are phylogenetic when they have to do with species and genera, and ecological when they relate to life-forms and habitat-forms. It is probable that these are all ecological responses, and that species and genera are more remote in origin and hence their ecologic significance less evident. Life-forms are less remote and their dependence upon the habitat more evident, while habitat-forms are mostly of more recent origin and their relation to the habitat obvious. This view seems to be supported by the fact that it has proved impossible to make a system of life-forms which is not based in part upon taxonomic forms and in part upon habitat-forms. All of these criteria permit still finer analysis, as species into varieties and forms, and habitat-forms into those produced by local or minute habitats. The experimental study of species and life-forms is still too slight for such a procedure, and it is possible as yet with

only a small number of habitat-forms. The consideration of indicator criteria is based upon the following divisions: (1) species and genera; (2) life-forms; (3) habitat-forms; (4) growth-forms; (5) communities.

Species and genera.—Quite apart from the life-forms and habitat-forms that they exhibit, species and genera, and to some extent families also, have an indicator value dependent upon their systematic position. The latter is determined primarily by the responses recorded in the reproductive structures at a time relatively remote. Their indicator meaning is consequently often obscure, and this obscurity is increased by a complete lack of experimental knowledge as to the factors which originate reproductive characters. Thus, while many species and genera show correlations with habitat or climate, this is chiefly on the side of vegetative responses, such as the relation of the *Nymphaeaceae* to bodies of water. They often exhibit, however, a valuable indirect correlation with climate due to origin and migration. This is the basis of floristic studies such as those of Sendtner (1856), Drude (1890), and others, and of the more exact floristic methods of Jaccard (1901-1914) and Raunkiaer (1905-1916). The value of these must remain statistical and general until they are related to successional movements and to measured physical factors.

Species and genera acquire their chief significance by virtue of the ecological values involved in phylogenetic relationship. This is obviously true of all genera which are largely or wholly consistent as to life-form, and it holds to a considerable degree for all others. Habitat, successional, and indicator values are concerned in this, and the genus thus becomes a sign of a more or less definite ecological complex of responses. This is likewise true of species in the general sense employed by Linné and Gray. A genus consists of several to many species because of the diverging evolution of an original stock under the more or less direct control of changing habitats. A species shows a similar evolution of forms, distinguishable from each other but mutually related to each other by descent, as are the species of a genus. For the ecologist, the relationship of such forms to the parent species is fully as important and even more significant than their recognition. It is imperative for his purposes that this relationship to the species be shown by the name as the latter shows that of species to the genus. This demands the use of trinomials, which is in accord with the general practice of ornithologists and mammalogists, but contrary to that of many systematic botanists. The one disadvantage of the trinomial is length, but this is readily obviated by using merely the initials of the specific name, *e. g., Achillea m. lanulosa, Ranunculus f. reptans, Galium b. scias* (Clements, 1908:263; Clements and Clements, 1913). This has long been the well-known practice of mammalogy and ornithology, *e. g., Citellus t. parvus, Lepus c. melanotis, Cyanocitta s. frontalis, Butea b. calurus,* etc. This or a similar method is inevitable if systematic biology is to aid and not hinder the development of ecology and the closely related practical sciences of agriculture, horticulture, forestry, plant pathology, economic zoology, etc. Three reasons would appear to lead irresistibly to this result. The field worker must deal with units which are recognizable in the field with a fair exercise of patience and keenness. He must carry in mind the names and characteristics of a large number of species, and he can do this only by relating them to each other. There is a very definite limit to the capacity of the average memory,

and this limit is greatly overstepped by a system which trebles the total number of species in a region and substitutes for a clearly marked genus like *Astragalus* 19 genera recognizable with difficulty by the systematist and practically impossible for others. Finally, while the ecologist is willing to go even farther than the systematist in recognizing minor differences, providing these are based upon statistical field studies and experiment and not upon herbarium specimens, the practical scientist is concerned primarily with real species rather than the many varieties and forms into which some of them fall. At least, when the need for a closer knowledge arises in a particular case, it is infinitely easier and more helpful to deal with the variations of a well-recognized species than with a dozen binomials, none of which to him have the slightest relation to each other.

If taxonomy is to be helpful to anyone but taxonomers, it must clearly do several things. It must recognize the field as the only adequate place for determining new forms, and must commit itself unreservedly to the methods of statistical and experimental study. It must restrict the use of the binomial to species in the Linnean and Grayian sense and employ the abbreviated trinomial for all segregates of such species, except in the rare cases where a coordinate species has been overlooked. It must realize that the splitting of genera only places so many stumbling-blocks in the way of all non-systematists, and makes them still more unsympathetic with such methods. Finally, it must recognize that a manual which can be used with success only by the systematist fails signally in its purpose, and be willing to construct keys and descriptions primarily for foresters, agronomists, grazing ecologists, and others whose knowledge of taxonomy is slight. Upon such a basis, species and genera will not only have vastly greater usefulness, but greater significance also to the ecologist, and he will be encouraged to do his share by handling them with greater accuracy and certainty (Hall and Clements, 1923).

LIFE-FORMS.

History.—The concept of the life-form was first formulated by Humboldt (1805:218), who used the term vegetation-form. Under various names, the concept has since been employed by many plant geographers and ecologists and several have proposed more or less complete systems of classification. Grisebach (1872), like Humboldt, based vegetation-forms upon physiognomy, and both systems have in consequence little more than historical value to-day. Warming (1884) and Reiter (1885) contributed many of the essentials of the modern systems, but these probably owe more to Drude (1890, 1896) than to anyone else. Krause proposed a classification in 1890 and Pound and Clements (1898) modified that of Drude somewhat in applying it to American vegetation. For this reason it is proposed to treat the latter here in detail, as well as the more recent systems of Raunkiaer (1903-1907), Warming (1908-1909) and Drude (1913). It will readily be seen that all of these have much in common, though this is not obvious in Raunkiaer's classification, which is based mainly upon adaptation for overwintering. All of them are founded more or less upon the two principles enunciated by Drude, namely, (1) the rôle played by a particular species in vegetation and (2) its life-history under the conditions prevailing in its habitat, with especial reference to duration, protection, and propagation. In the following discus-

sion life-form is used as the general term to include vegetation-forms, habitat-forms, growth-forms, etc.

Pound and Clements, 1898-1900.—As indicated above, the system employed by Pound and Clements in the "Phytogeography of Nebraska" (1898:45; 1900:95; cf. Clements, 1902:616) was essentially the earlier system of Drude (1896) modified to fit the vegetation of a prairie State. It possessed some intrinsic interest in that the entire flora of the State was passed in review from the standpoint of the various groups, and with reference to the general conditions of the different habitats (1900:95-312). Vegetation-forms were arranged in 7 main groups, which were divided into 34 minor ones. This system was used by Clements and Clements in "Herbaria Formationum Coloradensium" in 1902 and "Cryptogamae Formationum Coloradensium" in 1906.

I. Woody plants.
- 1. Trees.
- 2. Shrubs.
- 3. Undershrubs.
- 4. Climbers and twiners.

II. Half shrubs.
- 5. Half shrubs.

III. Pleiocyclic herbs (perennials).
- 6. Rosettes.
- 7. Mats.
- 8. Succulents.
- 9. Creepers and climbers.

Turf-builders.
- 10. Sod-formers.
- 11. Bunch-grasses.

Rhizomata.
- 12. Rootstock plants.
- 13. Bulb and tuber plants.
- 14. Ferns.

IV. Hapaxanthous herbs.
- 15. Dicyclic herbs (biennials).
- 16. Monocyclic herbs (annuals).

V. Water plants.
- 17. Floating plants.
- 18. Submerged plants.
- 19. Amphibious plants.

VI. Hysterophytes.
- 20. Saprophytes.
- 21. Parasites.

VII. Thallophytes.
- 22. Mosses.
- 23. Liverworts.
- 24. Foliaceous lichens.
- 25. Fruticulose lichens.
- 26. Crustaceous lichens.

Fungi.
- 27. Geophilous fungi.
- 28. Xylophilous fungi.
- 29. Biophilous fungi.
- 30. Sathrophilous fungi.
- 31. Hydrophilous fungi.
- 32. Entomophilous fungi.

Algae.
- 33. Filamentous algae.
- 34. Coenobioid algae.

Raunkiaer, 1905.—The system of Raunkiaer (1905 : 347) seems on the surface to differ radically from all others. This is due to the fact that the winter protection of buds is assigned the first rank and the growth-form during the vegetative season is regarded as secondary. The apparent difference is increased by the use of new terms based upon the degree of bud protection. As a matter of fact, Raunkiaer's system, like the others discussed here, takes account of both summer and winter conditions, and its difference is more a matter of arrangement and terminology than of essentials. For example, the group of phanerophytes corresponds essentially to woody plants, cryptophytes constitute the bulk of pleiocyclic herbs, and therophytes are annuals, while the subdivisions practically all have their equivalents in the other systems. The hemicryptophytes are far from satisfactory as a group, because of their similarity to helophytes on the one hand (p. 420) and therophytes on the other (p. 423). By the omission of cryptogams, the classification avoids confusion with systematic types and presents an attractively consistent character, increased by a consistent terminology. While the terms are

well-chosen and properly constructed, their length will preclude their common use, except perhaps in the case of the five major groups:

I. Phanerophytes (bud-shoots aerial):
1. Herbaceous phanerophytes.
2. Evergreen megaphanerophytes (above 30 m.) without bud-scales.
3. Evergreen mesophanerophytes (8 to 30 m.) without bud-scales.
4. Evergreen microphanerophytes (2 to 8 m.) without bud-scales.
5. Evergreen nanophanerophytes (below 2 m.) without bud-scales.
6. Epiphytic phanerophytes.
7. Evergreen megaphanerophytes with bud-scales.
8. Evergreen mesophanerophytes with bud-scales.
9. Evergreen microphanerophytes with bud-scales.
10. Evergreen nanophanerophytes with bud-scales.
11. Phanerophytes with succulent stem.
12. Deciduous megaphanerophytes with bud-scales.
13. Deciduous mesophanerophytes with bud-scales.
14. Deciduous microphanerophytes with bud-scales.
15. Deciduous nanophanerophytes with bud-scales.

II. Chamaephytes (bud-shoots protected by snow or fallen leaves):
16. Suffrutescent chamaephytes: many Labiatae.
17. Passive decumbent chamaephytes: species of Sedum, Saxifraga.
18. Active chamaephytes: Linnaea, Empetrum.
19. Cushion plants: Azorella, Raoulia.

III. Hemicryptophytes (bud-shoots at the soil level):
20. Protohemicryptophytes.
    A. Plants without creeping offshoots: Linaria, Verbena, Medicago.
    B. Plants with creeping offshoots, stolons, or rhizomes: Urtica, Saponaria.
21. Subrosette plants.
    A. Plants without creeping offshoots: Caltha, Geum.
    B. Plants with creeping offshoots: Ranunculus reptans.
22. Rosette plants.
    A. Plants without offshoots: Primula, Taraxacum, Carex.
    B. Plants with offshoots: Hieracium, Petasites.
    Plants with monopodial rosette.
    I. Monopodium with leaves but no scales.
        A. Aerial leaf and flower shoots: Trifolium pratense.
        B. Aerial shoots flower-bearing only.
            a. Without creeping offshoots: Plantago major.
            b. With creeping offshoots: Fragaria, Trifolium repens.
    II. Monopodium with both leaves and scales.
        A. Without creeping offshoots: Anemone hepatica.
        B. With creeping offshoots: Convallaria majalis.
    III. Monopodium with scales alone: Sedum rhodiola.

IV. Cryptophytes (bud-shoots buried in the soil):
Geophytes:
23. Rhizome geophytes: Polygonatum.
24. Tuber geophytes: Cyclamen.
25. Tuberous root geophytes: Orchis.
26. Bulb geophytes: Allium, Lilium.
27. Root-bud geophytes: Cirsium arvense, Moneses.
28. Helophytes: Typha, Scirpus, Equisetum, Sagittaria.
29. Hydrophytes: Nymphaea, Zostera, Hippuris, Potamogeton.

V. Therophytes (3); annuals: Galium aparine, Thlaspi arvense.

Warming, 1908.—Warming (1909 : 5) has based his outline of growth-forms upon the following principles:

"Just as species are the units in systematic botany, so are growth-forms the units in oecological botany. It is therefore of some practical importance to test the possibility of founding and naming a limited number of growth-forms upon true oecological principles. It can not be sufficiently insisted that the greatest advance not only in biology in its wider sense, but also in oecological phytogeography, will be the oecological interpretation of the various growth-forms: From this ultimate goal we are yet far distant.

"It is an intricate task to arrange the growth-forms of plants in a genetic system, because they exhibit an overwhelming diversity of forms and are connected by the most gradual intermediate stages, also because it is difficult to discover guiding principles that are really natural. Nor is it an easy task to find short and appropriate names for the different types. Genetic relationships and purely morphological or anatomical characters such as the venation and shape of leaves, the order of succession of shoots, monopodial and sympodial branching, are of very slight oecological or of no physiognomic significance. Oecological and physiological features, particularly the adaptation of the nutritive organs in form, structure, and biology, to climate and substratum, or medium, are of paramount importance. Cases are not wanting, however, in which oecological grouping runs parallel with systematic classification.

"In the case of the polycarpic plants it is necessary to consider, first, their adaptation to climate, and in particular the season unfavorable to plant life; secondly, the vegetative season; and finally the conditions prevailing in regard to the soil, which Schimper terms *edaphic* conditions. Of greatest importance is—

"1. *Duration of the vegetative shoot:* Lignified axes of trees, shrubs, and under-shrubs; perennial herbaceous shoots; herbaceous shoots deciduous after a short period.

"And closely associated with this is—

"2. *Length and direction of the internodes:* Whether the shoots have short internodes (rosette-shoots) or long internodes, and whether the latter are erect (orthotropous) or prostrate and creeping (plagiotropous).

"3. *Position of the renewal buds* during the unfavorable season high up in the air, near the soil, under the surface of the soil, or buried in the soil (geophilous).

"Of less importance is—

"4. *Structure of the renewal-buds or of buds in general.*

"5. *Size of the plant* is of some moment, not only because in the struggle for existence the taller plants are enabled to establish a supremacy more easily, but also because they are more exposed to the inclemency of climate; shrubs reach greater altitudes and latitudes than trees, while dwarf shrubs and herbs extend even further than shrubs.

"7. *The adaptation of the assimilatory shoot to the conditions of transpiration.*

"8. *The capacity for social life* is of great importance in the struggle between species and consequently in the composition and physiognomy of the plant-community. This capacity is due in some cases to the prolific production of seed, but usually to more vigorous vegetative multiplication by means of traveling shoots, or shoots given off from the root. And this latter is to some extent determined by the soil (moist or wet soil, loose sandy soil, etc.)."

Warming divides growth-forms into six classes and subdivides these into subclasses and types as follows:

1. Heterotrophic growth-forms: holoparasites and holosaprophytes.
2. Aquatic growth-forms.
3. Muscoid growth-forms.
4. Lichenoid growth-forms.
5. Lianoid growth-forms.
6. All other autonomous land-plants.
   I. Monocarpic herbs.
      (*a*). Aestival annual plants.
      (*b*). Hibernal annual plants.
      (*c*). Biennial-perennial herbs.
   II. Polycarpic plants.
      (*a*). Renascent herbs.
         (1) Herbs with multicipital rhizomes: Silene inflata.
         (2) Mat-geophytes.
            a. With stem-tubers: Crocus.
            b. With root-tubers: Ophrydeae.
            c. With bulbs: Liliaceae.
            d. With perennial tuberous stem: Cyclamen.
         (3) Rhizome-geophytes.
            a. On loose soil of dunes: Ammophila, Carex.
            b. On loose humus soil in forests: Polygonatum, Anemone nemorosa.
            c. On mud in water or swamp: Phragmites, Hippuris.
      (*b*). Rosette-plants.
         (1) Leaves sessile, elongated: Plantago, Taraxacum.
         (2) Leaves long-stalked, broad: Anemone, Hepatica.
         (3) Leaves succulent: Crassulaceae.
         (4) With runners: Fragaria, Potentilla anserina.
         (5) Flowers on leafy shoots: Alchemilla, Geum.
         (6) Flowers on leafless shoots: Primula.

6. All other autonomous land-plants—*cont.*
   II. Polycarpic plants—*continued.*
      (*b*) Rossette-plants—*continued.*
         (7) Grass-rosettes: grasses, sedges, Eriocaulaceae.
         (8) Musa-form: gigantic tropical herbs (banana).
         (9) Tuft-trees.
            1. Trunks without secondary growth; leaves large and divided: tree-ferns, palms, cycads.
            2. Trunks with secondary growth; leaves undivided, linear; Yucca, Dracaena.
            3. Strelitzia-form.
      (*c*) Creeping plants.
         (1) Herbs: Lycopodium clavatum, Menyanthes.
         (2) Dwarf shrubs: Arctostaphylus uva-ursi, Linnaea.
         (3) Jungermannia-form.
      (*d*) Land-plants with long, erect, long-lived shoots.
         (1) Cushion-plants: Silene acaulis, Azorella.
         (2) Undershrubs:
            1. Labiate type: Salvia, Thymus, Artemisia.
            2. Acanthus type: Acanthaceae.
            3. Rhizome-undershrubs: Vaccinium myrtillus.
            4. Cane-undershrubs: Rubus idaeus.
            5. Soft-stemmed plants: Araceae.
            6. Cactus-form: Cactaceae, Stapelia.
            7. Woody plants with long-lived lignified stems, canopy-trees, shrubs, dwarf shrubs.

Drude, 1913.—In broadening his earlier classification into a universal system of life-forms, Drude (1913:29) has applied the following criteria:

1. The basic form (tree, shrub, annual or perennial herb), by the organization of which for a long period of years, or for a single season of growth, each plant maintains its own place. The method of propagation is an essential part of this basic form.
2. The form and duration of the leaves.
3. The protective devices of leaf- and flower-shoots during the period of rest.
4. Position and structure of the organs of absorption.
5. Flowering and fruiting in relation to reproduction as a single or recurrent process.

On this basis, Drude makes three great divisions in which he recognizes 55 types and many subtypes.

I. Aerophytes (woody plants, perennial and annual herbs).
1. Monocotyl tuft-trees: Sabal, Yucca.
2. Monocotyl palm shrubs and lianes: Bactris, Calamus.
3. Dwarf palms: Nipa.
4. Tree-ferns and cycads: Cyathea, Cycas.
5. Needle-leaved woody plants.
6. Dicotyl trees.
7. Dicotyl shrubs and bushes.
8. Dicotyl woody lianes.
9. Mangrove-form.
10. Lobelia-form.
11. Tree-grasses: Bambusa.
12. Smilaceous bushes and lianes: Smilax, Ruscus.
13. Leafless dicotyl rushwood and thorn bushes: Casuarina, Ephedra, Spartium.
14. Few-leaved columnar woody plants: Adenium, Tumboa.
15. Stemmed evergreen rosette succulents: Agave, Sempervivum.
16. Dicotyl stem succulents: Cactaceae.
17. Dicotyl dwarf shrubs: Calluna, Artemisia, Dryas.
18. Woody parasites: Loranthus.
19. Monocotyl giant herbs: Musa, Bromelia.
20. Monocotyl root-climbers: Monstera.
21. Rosette ferns and cycads: Aspidium.
22. Tuber-stemmed epiphytes: Bulbophyllum, Myrmecodia.
23. Perennial and renascent grasses: Andropogon, Poa, Carex.
24. Sedges and rushes with suppressed leaves: Juncus, Scirpus.
25. Erect half-shrubs: Ruta.
26. Half-shrubs with creeping stems or offshoots: Linnaea.
27. Dicotyl cushion-plants: Raoulia, Silene acaulis.
28. Succulent cushion-plants: Aloe, Mesembryanthemum.
29. Biennial and perennial rosettes: Pulsatilla, Verbascum.
30. Renascent and annual climbers: Dioscorea, Ipomoea.
31. Renascent multicipital herbs: Peucedanum, Galium.
32. Geophilous rootstock plants: Iris, Circaea, Equisetum.

I. Aerophytes (woody plants, perennial and annual herbs)—*continued.*
33. Geophilous tuber plants: Orchis, Cyclamen.
34. Geophilous bulb plants: Allium, Oxalis.
35. Monocotyl therophytes: Eragrostis.
36. Dicotyl therophytes: Chenopodium.
37. Dicotyl short-lived herbs: Koenigia.
38. Saprophytic and parasitic herbs: Corallorhiza, Monotropa, Cuscuta.

II. Water plants:
39. Amphibious slime-rooted plants with aerial leaves: Sagittaria, Nelumbo, Marsilea, Equisetum.
40. Amphibious free-swimming plants with aerial leaves: Pistia, Eichhornia.
41. Amphibious plants rooting on stones: Podostemaceae.
42. Hydrophytes with rooting axis and immersed leaves: Isoetes, Zostera, Lobelia.
43. Hydrophytes with rooting axis and floating leaves: Potamogeton, Nymphaea.
44. Free-swimming hydrophytes: Lemma, Utricularia, Azolla.

III. Life forms of mosses and thallophytes:
A. Aerophytes:
45. Terrestrial cushion-mosses: Leucobryum.
46. Terrestrial tall-stemmed mosses: Polytrichum.
47. Terrestrial and epiphytic mat-mosses: Hypnum, Frullania.
48*a*. Petrophilous creeping mosses, chiefly liverworts: Marchantia, Jungermannia.
48*b*. Petrophilous mat- and cushion-mosses: Georgia, Andreaea.

B. Hygrophytes and hydrophytes:
49. Bog mosses: Sphagnum.
50*a*. Streaming mosses: Fontinalis.
50*b*. Forming mats in water: Aneura, Scapania.
51. Epiphytic lichens: Usnea.
52. Fruticose and foliose lichens on rocks and earth: Cetraria, Umbilicaria, Cladonia.
53. Crustose lichens: Lecanora.
54. Forms of marine algae, green algae, bluegreen algae, etc.
55. Forms of saprophytic and parasitic fungi.

Comparison of the systems.—The three systems of Raunkiaer, Warming, and Drude differ greatly as to the manner of classification, but they are in much greater harmony as to the essential basis. Drude, however, constantly

uses taxonomic criteria, though he is very far indeed from consistent, separating monocotyls, dictoyls, and ferns sometimes into distinct types, sometimes into subtypes, and then frequently uniting two of them or all three into the same type or subtype. Raunkiaer ignores taxonomy altogether and Warming practically does the same, with the exception of the thallophytic forms, in which taxonomic form and life-form are more or less identical. The treatment of aquatics, in which the impress of the habitat is marked, is very different in the three cases. Raunkiaer makes helophytes and hydrophytes two types of cryptophytes, coordinate with geophytes. Warming treats aquatic plants as one of his six main divisions, though he considers them under ecological classes or habitat-forms (136), while Drude makes water plants one of his two great divisions of flowering plants and recognizes three amphibious and three aquatic types. Raunkiaer uses bud-position as the primary criterion for his five main groups (all flowering plants and ferns). Warming employs systematic criteria for two of his six divisions, ecologic for three, and physiologic for one. Land-plants are divided upon the nature of the life-period into monocarpic and polycarpic. Drude's first division is ecologic for aerophytes, and water-plants, and systematic for mosses and thallophytes. In all three systems the types and subtypes are frequently the same, except that Drude usually divides the same type or subtype upon the basis of taxonomy.

The systems of Raunkiaer and Drude are the most unlike, while Warming's occupies an intermediate position. Raunkiaer's classification is much the most compact and consistent, probably because he has adhered to one criterion throughout. Because of this, and because he has given definite names to practically every type, it is also much more usable. In fact, its great merit lies in the possibility of using it as a sort of climatic index, while the other two systems merely classify a great mass of plants in the usual static fashion. As Warming points out, Raunkiaer's system has one disadvantage in that it fails to take account of the growing season response (1906:6) and hence applies to the flora and not to the vegetation of a region or country.

Vegetation-forms.—For our purpose, much the most useful and consistent view of life-forms is obtained from a single point of view, that of vegetation. The development and structure of vegetation are chiefly a matter of dominants and subdominants, and it is the life-forms shown by these which are of paramount importance. Hence it becomes desirable to speak of them as vegetation-forms, as Drude did originally, following Grisebach and Humboldt. For practical purposes, it is undesirable to make a complete classification of vegetation-forms and the latter is carried only so far as the demands of indicator vegetation warrant.

The dominance of a species depends upon the perfection of its methods of increase on the one hand, and upon the success of its vegetative shoots in competition on the other. While the latter is partly a matter of length of shoot and rate of growth, it is chiefly one of carrying the shoots of one season over to the next. A wholly consistent and usable system is possible upon the basis of these three processes. It avoids the complexities and uncertain correlations introduced by taxonomy and permits a consistent treatment of habitat-forms with their more evident factor correlations. It contains the

essentials of the systems discussed above, inasmuch as Drude states that the basic life-forms are trees, shrubs, perennial and annual herbs, Warming divides his group of land-plants into monocarpic and polycarpic, while Raunkiaer's largest groups, phanerophytes, cryptophytes, and therophytes, practically correspond to woody plants, perennial and annual herbs. In giving more or less equal value to the life-period, method of over-wintering, and conservation of shoots and success in competition, it appears desirable to recognize four coordinate groups, viz., annuals, biennials, herbaceous perennials, and woody perennials, characterized as follows:

1. *Annuals:* Passing the winter or dry season in seed or spore form alone; no propagation or accumulation of aerial shoots; living one year.
2. *Biennials:* Passing one unfavorable season in the seed or spore form, and the next as a propagule; no accumulation of aerial shoots; living two or parts of two years.
3. *Herbaceous perennials:* Passing each unfavorable season in both seed or spore and propagule form; no accumulation of aerial shoots; living several to many years.
4. *Woody perennials:* Passing each unfavorable season as seeds or spores, and aerial shoots or masses, often with propagule forms also, especially when injured; living many seasons as a rule.

Each of these divisions is thoroughgoing and all forms of annual habit are placed in the first group, whether flowering plants, mosses, or fungi, just as perennials are placed in their respective group regardless of their systematic position or habitat-form. The varying nature of the four groups makes it obviously impossible to employ the same criterion for the division into types. For annuals and biennials, the form of the aerial plant body is probably of first importance and the size next, while for woody plants height is perhaps most decisive, leaf-character next, and form last. While perennial herbs usually show the most marked differences in the propagules, the form of the aerial shoot is often even more distinctive, and both criteria must be employed as occasion warrants. The final result is a simple compact system, closely resembling the earlier one of Drude (1896; Pound and Clements, 1900) and different but little in essence from that of Raunkiaer. For the study of indicators only the major divisions appear to be of value at present, and these alone are given in the outline.

1. Annuals.
2. Biennials.

Herbaceous perennials:

3. Sod-grasses.
4. Bunch-grasses.
5. Bush-herbs.
6. Cushion-herbs.
7. Mat-herbs.
8. Rosette-herbs.
9. Carpet-herbs.
10. Succulents.

Woody perennials.

11. Halfshrubs.
12. Bushes.
13. Succulents
14. Shrubs.
15. Trees.

Indicator significance of vegetation-forms.—It is obvious that the vegetation-forms of climax dominants are indicators of climate. This has long been recognized as the basis for the climatic zones of continents and mountains. The same principle applies to climax formations generally; and these are accordingly taken as indicators of the major climates of the globe (Clements, 1916). This close correlation between the major vegetation-forms and climate as expressed in progressively favorable conditions of temperature and moisture is paralleled by the succession of vegetation-forms in the development of a climax. In the development of a sere, extreme conditions as to water yield to those more and more favorable to growth, and this change is accompanied by a sequence of dominants belonging to successively higher vegeta-

tion-forms. In short, the more striking indicator values of succession are afforded by the changes from one vegetation-form to another, just as those next in importance are marked by the change from one associes to another of the same form. Moreover, while the exact significance of any species can be known only by determining its functional response to the factors of its habitat, its general meaning is indicated by the vegetation-form to which it belongs.

Raunkiaer (1905, 1908; Smith, 1913:16) has employed his system of vegetation-forms to determine the climatic relations of a particular flora. He establishes a hypothetical *normal spectrum* for the whole earth by selecting 1,000 representative species, of which 400 were carefully analyzed. The *biological* or *phyto-climatic* spectrum of a particular region is obtained by finding the percentage of species belonging to each life-form. Raunkiaer's method adds interest and detail to the long-accepted relations between climate and flora. It can not be applied to vegetation and hence it has no real indicator value, as is shown by the author's own statements (1905:433):

"If we consider the flora of Denmark, it is characterized from the botano-climatic viewpoint by its hemicryptophytes and not by its phanerophytes, for, however important may be the rôle played by the forests in the vegetation of Denmark, the small number of species of phanerophytes is significant of the conditions offered by this region: The species of phanerophytes represent but 6 to 7 per cent of those living in Denmark, while the hemicryptophytes constitute nearly a half of all the species.

"But from the standpoint of the formation, the phanerophytes, or trees, dominate by their size wherever one finds them. In spite of the inferiority in number of the species of phanerophytes to those of hemicryptophytes or cryptophytes, our forests belong to the phanerophytic formations because the phanerophytes they contain dominate the other components of the forests."

HABITAT-FORMS.

Concept and history.—In addition to the taxonomic form and vegetation-form, species exhibit a form which is much more distinctly related to the habitat. These usually bear the clear impress of the latter and hence are called habitat-forms. The fuller recognition of their basic importance by Warming (1895, 1896:116) was largely responsible for the rapid development of ecology during the last two decades. Unlike taxonomic forms and vegetation-forms, their value is primarily ecological and not floristic, and they are of correspondingly greater importance as indicators. Their significance lies in the fact that they bear the primary impress of the controlling or limiting factor, and thus serve as direct indicators of the critical factors of the habitat. They are the essential basis of all indicator values, and must be regarded as the main objective in all such studies.

Warming's system.—Warming (1896 : 116) was the first to adequately organize the four universally known groups of habitat-forms, namely, hydrophytes, xerophytes, halophytes, and mesophytes (cf. Clements, 1904:20). Pound and Clements (1898:94; 1900:169), feeling the need of recognizing light as well as water, divided mesophytes primarily upon the basis of light and combined halophytes with xerophytes, thus establishing the following six groups: hydrophytes, mesophytes, hylophytes, poophytes, aletophytes, and xerophytes. This division of mesophytes retained some idea of life-forms,

and it was later dropped (1902:166; 1907:183) for the consistent light grouping of mesophytes into *heliophyta, sciophyta,* and *scotophyta,* corresponding essentially to Schouw's classification into sun, shade, and darkness plants (1823:166). A detailed classification of habitat-forms was made by Clements (1902:5-14), in which light, solutes, aeration, and other factors were taken into account, but with water-content as the primary basis. The 64 subdivisions were largely successional and physiographic, and this number can be greatly reduced if factors alone are considered. This is essentially what Warming has done in his most recent grouping of formations (1909: 136), which also represents much the best classification of habitat-forms up to the present. This system is as follows:

A. The soil (in the widest sense) is very wet, and the abundant water is available to the plant; the formations are therefore more or less hydrophilous:
- Class 1. Hydrophytes (of formations in water).
- Class 2. Helophytes (of formations in marsh).

B. The soil is physiologically dry, *i. e.*, contains water which is available to the plant only to a slight extent; the formations are therefore composed essentially of xerophilous species:
- Class 3. Oxylophytes (of formations on sour (acid) soil).
- Class 4. Psychrophytes (of formations on cold soil).
- Class 5. Halophytes (of formations on saline soil).

C. The soil is physically dry, and its slight power of retaining water determines the vegetation, the climate being of secondary import; the formations are therefore likewise xerophilous:
- Class 6. Lithophytes (of formations on rocks).
- Class 7. Psammophytes (of formations on sand and gravel).
- Class 8. Chersophytes (of formations on waste land).

D. The climate is very dry and decides the character of the vegetation; the properties of the soil are dominated by climate; the formations are also xerophilous:
- Class 9. Eremophytes (of formations on desert and steppe).
- Class 10. Psilophytes (of formations on savannah).
- Class 11. Sclerophyllous formations (bush and forest).

E. The soil is physiologically or physically dry:
- Class 12. Coniferous formations (forest).

F. Soil and climate favor the development of mesophilous formations:
- Class 13. Mesophytes.

Modifications of Warming's system.—In making use of habitat-forms as indicators in North American vegetation, a few modifications of the above groups are desirable. These are perhaps further warranted by some advance in ecological knowledge in the ten years since Warming made the following statement concerning habitat-forms (1909:133):

"When endeavoring to arrange all land-plants, omitting marsh-plants, into comprehensive groups, we meet with first some communities that are evidently influenced in the main by the physical and chemical characters of the soil which determine the amount of water therein; secondly, other communities in which extreme climatic conditions and fluctuations, seasonal distribution of rain and the like, decide the amount of water in soil and character of vegetation. In accordance with these facts, land-plants may be ranged into groups, though in a very uncertain manner. The prevailing vagueness in this grouping is due to the fact that *oecology is only in its infancy,* and that very few detailed investigations of plant-communities have been conducted, the published descriptions of vegetation being nearly always one-sided and

floristic, as well as very incomplete and unsatisfactory from an oecological standpoint."

The terms employed are those suggested by Clements (1902:5) and adopted by Warming for most of his divisions:

I. Hydrophytes: Chresard maximum to very high, the soil being water or covered with water; climate usually moist.
1. Emophytes: Entire plant submerged; no transpiration or functional stomata.
2. Plotophytes: Plant floating, at least the leaves; transpiration and stomata on upper surface of leaves at least.
3. Helophytes: Amphibious, rooted in water or mud; transpiration high and stomata on both surfaces, the stem often functioning as a leaf.

II. Mesophytes: Chresard medium, soil moist; climate moist; transpiration high to medium.
4. Heliophytes: Sun-plants, growing in sunlight or light stronger than 0.10.
5. Sciophytes: Shade-plants, growing in light less than 0.10.

III. Xerophytes: Chresard low, soil physically or physiologically dry, climate usually dry, or various; transpiration low.
A. Soil physiologically dry, climate various:
6. Halophytes: Chresard low, due to an excess of soil salts.
7. Psychrophytes: Chresard low, due to cold soil or to ice.
8. Oxyphytes: Chresard low, due to lack of oxygen in the soil.
B. Soil physically dry, climate various:
9. Lithophytes: Chresard low, due to a rock matrix.
10. Psammophytes: Chresard low, due to sandy or gravelly soil.
11. Chersophytes: Chresard low, due to a rock substratum.
C. Climate dry and soil physically dry in consequence:
12. Eremophytes: desert plants, chresard low or lacking much of the year.
13. Psilophytes: grassland plants (prairie, plains, steppes), chresard low some of the year.
14. Drymophytes: bushes, shrubs, and small trees, mostly sclerophyll scrub, chaparral, and woodland; chresard low or discontinuous.

The changes from Warming's system lie in the subdivision of hydrophytes and mesophytes, well-recognized distinctions of which Warming himself makes use (18, 165), in the distribution of conifers among helophytes, mesophytes, psammophytes, and drymophytes, in the line drawn between desert and grassland plants, and in treating the bush-shrub form as primary and the division into sclerophyll and deciduous types as secondary.

Indicator value.—Habitat-forms are the most satisfactory of all indicator-forms. This is chiefly because of their obvious response to the controlling factors which the forester, grazing expert, and others must deal with. This is partly also because they mark out a definite area in which these factors prevail. For all practical purposes in a particular region, habitat-forms constitute the ground-work of an indicator system. This is evident when it is realized that the fourteen groups comprise all dominants and thus each habitat-form has a community value as well. When reinforced by vegetation-forms in so far as their significance for climate is known, and by ecads and growth-forms for the more recent or the minor effects of physical factors, habitat-forms afford a nearly complete system of indicators for the practical application of biology. It is still necessary to interpret some of them with greater accuracy and certainty. This will come about from the quantitative study of their physiologic response, permitting the closer correlation of form

and function, as well as by the increasing use of standard plants as even more accurate indicators.

Habitat-forms can be used to give a general statistical expression to the climatic or physiographic conditions of a region, and thus permit comparisons, much as Raunkiaer has used vegetation-forms. Their paramount value lies in their positive indication of definite local conditions on the basis of known correlation with measured factors. It should be noted that the mesophytes and the last three groups of xerophytes represent climax habitats and communities, while the hydrophytes and the first six groups of xerophytes characterize developmental stages. This is a natural outcome of the fact that the climate is controlling as to soil conditions in the former, while the climatic control is much reduced or is none at all for the latter. The general correlation of climax habitat-forms and their most important representatives with physical factors is given in "Plant Indicators" (p. 105), in so far as quantitative results are available.

In a recent paper, Raunkiaer (1916:225; cf. Fuller and Bakke, 1918:25) has sought to express the general relation of plants to climate by a series of leaf classes based upon size. Of the latter, he recognizes six kinds as follows: leptophyll, 25 sq. mm.; nanophyll, 9×25 sq. mm.; microphyll, $9^2 \times 25$ sq. mm.; mesophyll, $9^3 \times 25$ sq. mm.; macrophyll, $9^4 \times 25$ sq. mm.; megaphyll. While this classification will serve a useful purpose in drawing the attention of ecologists to such relations, it seems quite too subjective for final acceptance. This seems obvious from the author's difficulties as to compound and lobed leaves, and especially from the following statement (l. c., 29):

"Originally I multiplied by 10, but the resulting limits between the 'size-classes' did not seem as natural as when 9 was used. It is easy in the final analyses to separate the single classes into the groups of small, medium, and large."

Thus, while there can be little question that leaf-size often serves as an indicator of climate or habitat in some degree, it must be refined by means of leaf-number, thickness, structure, outline, and texture, and checked by quantitative studies of factors (cf. E. S. Clements, 1905:91).

Ecads.—An ecad is produced by direct and demonstrable adaptation to a habitat. It is a habitat-form in the making. The habitat-form, while capable of modification within certain limits, has recorded the impress of a particular habitat for so long that its general character is fixed and transmitted. An ecad, though it may show just as striking adaptation, is a recent product, and its character is not yet fixed and transmissible. The difference between the two is solely one of inheritance, and it seems probable that ecads become fixed and pass over into habitat-forms after a long residence in the same habitat. This is indicated by the behavior of alpine dwarfs, some of which retain their form when moved to lower altitudes or shifted to wetter alpine situations, while others at once change in response to the new conditions. The former have attained the stability of habitat-forms, the latter are ecads.

Because of its plastic nature, the ecad is a more exact and sensitive indicator than the habitat-form. Its structural change corresponds more nearly to the functional response and can be regarded as a measure of the latter to a

considerable degree. Its growth as well as its form is often characteristic, and its indicator value can be based upon both. One unique advantage of the ecad is that it is produced in abundance in nature, wherever habitats touch, especially where they recur constantly, as in mountain regions. A plastic species found in two or more habitats regularly shows an ecad corresponding to each. Similar results are readily obtained by transplanting such species to several different habitats. Ecads produced under definite quantities of water and light may be grown under control (Clements, 1905:157; 1919) and used for comparison with the natural ones (E. S. Clements, 1905) (plate 11).

Ecads have been classified and named with reference to habitats, as *hylocolus, psilocolus,* etc. (Clements, 1902:17; 1904:329). It seems much better to group and designate them with reference to the controlling factor (Clements, 1908: 263), as water ecads, light ecads, etc. Thus the general classification of ecads would necessarily correspond closely to that of habitat-forms, except in xerophytes, where the groups would be fewer. Such a classification would be of little value, however, since it is the relationship of the ecad to a particular species which is significant, as well as the number and kind of ecads actually occurring. A floating species, such as *Sparganium angustifolium,* forms both submerged and amphibious ecads, while *Nymphaea polysepala* has been seen to produce only amphibious ones. A plastic helophyte, such as *Ranunculus sceleratus,* or a mesophyte, such as *Achillea millefolium,* may give rise to several ecads. The same species may produce both water and light ecads, though as a rule a wide range of adaptation to the one factor is accompanied by a narrow range for the other. Under control it has been possible to produce ten distinct water ecads of *Ranunculus,* but beyond this point differences have to do chiefly with amount of growth rather than with structure. For the present, it is sufficient to recognize the controlling factor by designating ecads as hydrads, xerads, sciads, heliads, halads, etc., and to leave the question of a more exact terminology for the future. The importance of ecads in indicator work is so great that their recognition can no longer be neglected.

GROWTH-FORMS.

Nature.—While it is assumed that all plant forms are referable to the immediate or remote action of the habitat, this correlation is least certain for taxonomic forms. Its certainty increases progressively through life-forms and habitat-forms to reach a maximum in growth-forms. While Warming in particular has used this term in place of life-form and vegetation-form, the latter have the preference, both by priority and significance. But growth-form is such a desirable term for the immediate quantitative response made by a plant to different habitats or conditions that its retention in this sense seems well-warranted. As the direct visible response of the plant to physical factors, growth affords a more delicate scale of measurements even than the ecad. In fact, the latter is only a growth-form in which adaptation as shown by a qualitative change of form or structure is more striking than the quantitative difference in amount of growth. In the case of dwarfing, both changes usually occur together, and the growth-form differs from the ecad only in being the product of the conditions presented by a single season. If these

continue, the growth-form persists and becomes an ecad characteristic of the particular habitat. Thus, while the two forms may be measures of the same conditions, the one is an indicator of the annual variation, the other of the normal condition of the habitat. From the ecological side, it appears that growth-forms may become ecads, ecads become habitat-forms, and these finally fixed as vegetation-forms.

Kinds.—Every direct factor exerts an influence upon growth and produces corresponding growth-forms. Such factors are water, light, temperature, and aeration, and possibly certain solutes. Since all of these are concerned in the growth of each plant, it is possible to assign a particular one as the cause of any growth-form only when it is the controlling or limiting factor. In the majority of cases, the limiting action is evident, as with water in arid and semi-arid habitats or dry seasons, light in forests and thicket, temperature in high altitudes or latitudes or cold seasons, and aeration in wet areas or seasons. Maximum growth results when all four factors are at the optimum for a particular species. An apparent exception is afforded by the behavior of many species in moderate shade, but their height is usually offset by their slenderness, and the mass growth and dry weight are usually less than in the sun. With the optimum growth as the basis, it becomes possible to distinguish growth-forms due to the extremes of each factor, as well as to correlate different amounts of growth with known quantities of the limiting factor. In the case of water, growth is decreased by both an excess and deficit as a rule, but the former seems to operate through reduced aeration and lowered temperature. Similarly, growth is diminished by both high and low temperatures, but high temperatures act chiefly through the water relation. It is doubtful whether full sunshine as light ever inhibits growth, since photosynthetic activity decreases with any material reduction in light intensity. While many species are taller and more branched in moderate shade, it appears that mass growth is at a minimum and often becomes completely impossible with the increasing density of forest or thicket.

As a consequence of the above, it is most practical to distinguish four types of growth-forms, based upon the lack of the direct limiting factors, namely, those due to insufficient water, to insufficient heat, to shade, and to poor aeration. Since growth is primarily quantitative, each species will exhibit a series of forms from the optimum to the minimum, corresponding to each effective degree of change in the limiting factor. This relation lies at the base of ecological response and can only be determined experimentally. Two factors may act together in producing a growth-form, as in the case of alpine dwarfs due to drouth and low temperature. One factor may serve to emphasize another, as where the drouth of a desert is reinforced by an excess of salts in the soil, or it may decrease or counteract the effect of another, as is true of shade in arid regions. Finally, all four factors may be concerned causally in an effect produced directly by one of them. This is apparently the case in the death of sal seedlings in tropical forests, as shown by Hole and Singh (Chapter XIII). The immediate cause is poor aeration, due to the accumulation of soil-water as a consequence of lower temperature resulting from shade.

Indicator relations.—The growth of a species varies from one year to the next, and from one habitat to another. It often differs also in different por-

tions of the same habitat. In an area which is uniform physically, individuals frequently show striking variations due to competition. These four relations sum up the indicator values of growth-forms as they occur in nature and hence serve as the basis of all correlations. While they are well-known, little quantitative work has yet been done with them. This has been due to the time necessary to organize quantitative studies and methods out-of-doors and to focus these upon growth as the most basic of visible responses. Pearson (1918) has made measurements of the annual growth in height of yellow-pine seedlings for a period of six years and has found a close correlation with spring rainfall. Sarvis (1919) has clipped and weighed the growth on permanent grass quadrats at intervals of ten days and has made a general correlation with seasonal factors. Since species vary greatly in rate and amount of growth, it is desirable to select those most responsive to the habitat.

It is impossible to say as yet what type of growth is most readily correlated with seasonal variations or habitat differences. Theoretically, it seems that total growth as indicated by the dry weight of mature plants would furnish the best correlation (cf. Pearson, 1918; Frothingham, 1919; Sarvis, 1919). Actually, however, vegetative growth and reproductive growth make different demands, and are often antagonistic to each other. This is true to a large degree of the height-growth and width-growth of woody plants. The determination of dry weight is a practical impossibility for trees except when young, and the indicator correlation must be with growth directly. At present it is only possible to say that for the first 100 to 150 years height-growth offers the better correlation, and after this period growth in diameter reflects conditions more accurately. Mitchell (1918: 23) has shown in the case of incense cedar (*Libocedrus decurrens*) that the mean height-growth for the first 100 years was 65 feet, for the second century 28 feet, for the third 12 feet, and for the fourth 6 feet. The width-growth was 13 inches, 14 inches, 9 inches, and 5 inches for the same periods. Thus practically 60 per cent of the height-growth was made in the first century, and but 31 per cent of the width-growth, while the height-growth of the fourth century was but 5 per cent in contrast to a width-growth of 12 per cent. The correlation of reproductive growth and especially of seed-production with seasonal or habitat conditions is known only to the extent that it tends to rise with less favorable conditions as to water up to a certain point, as shown by alpine and arid regions. For most woody plants it is little or none in youth, and it increases steadily up to maturity. In the case of crop plants, it seems clear that the correlation with dry weight offers a satisfactory basis for comparison, though even here greater accuracy can be expected from the separate correlation of vegetative and reproductive growth with the controlling factors in the two periods.

Standard plants for growth correlations.—Because of the control possible as well as the opportunity for measuring functional responses, standard plants offer much the best method of establishing growth correlations. The value of the method increases as the standard plant approaches the one to be indicated in character, and reaches a maximum when the latter is itself employed as a standard, as in the use of yellow pine, Douglas fir, etc., in forest investigations. The employment of phytometers in this form is the most basic of all quantitative methods and is destined to play the paramount rôle in all exact studies of communities and habitats in the future.

Competition-forms.—The amount of a particular factor available for any species or individual is either determined by the habitat alone or by competition. In the great majority of cases, the major limits are fixed by the habitat, and within these competition determines the amounts available for each plant. Indeed, this is probably true of all communities except those initial ones in which the individuals are widely scattered. In nearly all cases, then, a growth-form is due partly to the nature of the habitat and partly to the modification of this by competition. The part played by each can be determined only by actual experiment or by the comparison of individuals growing in the same habitat but in areas with and without competition. Fortunately, such areas are of sufficient frequence in nature to reveal the normal growth-form of the habitat as well as the growth-form due to competition. A study of the chaparral and strand communities of southern California (Clements and Clements, 1916) disclosed an unusually large number of such competition-forms, especially among the annuals, as would be expected. While competition-forms are probably just as frequent among perennials, they are often much less striking.

As competition may occur in all degrees in accordance with the number and density of individuals, so there may be a complete series of forms from the normal to the extreme in which the plant never develops beyond the seedling stage before it dies. Under somewhat less severe competition, plants develop stems and leaves but fail to form flowers and fruit. In the next degree, reproduction occurs, but the flowers are single or few, while beyond this are more and more perfectly developed forms until the optimum for the habitat is reached. Each form is an index to some degree of competition, but its exact indicator value is more difficult to determine. This is due largely to the fact that competition has as yet received but little attention, especially on the experimental side. The view advanced by Clements (1904:166; 1905:310; 1907:251; 1916:72) that competition is purely physical seems to be confirmed by recent experiments. While it is perhaps unnecessary to rigidly exclude metaphor in connection with competition, it should be recognized that the experimental results so far obtained show that plants do not compete for "room." Competition has to do only with the direct factors of the habitat. Water and light are the factors universally concerned, though soil-air, nutrients, and heat must also be taken into account in particular habitats. In addition, there is often more or less decisive competition between the flowers of a community for pollination agents. Furthermore, the course of competition may be determined by a deleterious substance, especially a solute, which handicaps one species more than another. Such a handicapping influence is even more frequently represented by biotic agents, parasitic plants, rodents, grazing animals, etc.

The competition-forms commonly met with are due to competition for water or light, or for both together. There has been no experimental study of competition for soil-air or for nutrients, and it is impossible to assert at present that plants do compete for heat. Studies of germination under different densities of seeding suggest such competition for seedlings at least. No adequate study of competition-forms has been made, and hence it is impossible to relate them to definite quantities of water or light. In fact, it seems increasingly probable that the forms resulting from intense competition are

due to a lack of both factors, though in different degree. As a consequence, competition-forms can at present be used directly only as indicators of the general degree of competition. In connection with the habitat-form or ecad, they have an indirect value in making it possible to distinguish in indicators the direct effect of the habitat as contrasted with the added effect of competition.

COMMUNITIES AS INDICATORS.

Value.—The community as an indicator is a complex of all the preceding values. It derives its primary significance from the dominants, chiefly through their life-forms and ecological requirements. It includes the meanings of the less significant subdominants, and those of the much less important secondary species. In short, it is a complete scale upon which all the indications of the habitat are written. These values can be obtained only by analysis, however, and the latter leads at once to the study of dominants and subdominants, both climax and seral. The general principles of the latter have already been outlined under the sections on associational and successional bases. This leaves for consideration the various types of communities and the functions and structures they exhibit.

Kinds of communities.—With reference to association alone, three kinds of communities may be distinguished, viz., consocial,[1] associal, and mixed. The first consists of a single dominant, the second of two or more belonging to the same association or seral stage, and the third of dominants from different associations or associes. The basic indicator value of these is determined by whether they are climax or seral. The consocial community affords the most definite indication, while the associal type has the advantage of checking the indications of one dominant by those of the related ones. This is even truer in the case of mictia, but the indications are necessarily somewhat confused here, since one set of dominants is disappearing and the other increasing in number and importance. In this connection it is desirable to emphasize the fact that seral and climax communities furnish not only indications of existing factors and possibilities, but also of past and future ones. Each seral stage indicates the preceding stage and its habitat. The climax forecasts the consequences of any primary or secondary disturbance in it, and foreshadows the effects of climatic changes. As a result, both serve as invaluable indicators of the course and outcome of all possible human practices in them, and lend themselves to methods of scientific prophecy which can hardly be surpassed. A similar relation exists between consocial and associal communities. Wherever a consocies or consociation is found, the related dominants have occurred or can occur, at least with the slightest modification of the habitat. Thus, the indicator analysis of a community involves not only the measurement of existing conditions, but especially also a study of the linkage with the other communities of the sere or the climax. For indicator research, as in all serious ecological studies, any investigation which fails to take full account of successional and climax relations is inadequate, and at best can only lead to half-truths.

[1]This term is here used to refer to the community marked by a single dominant, whether consocies or consociation, and associal in a similar sense. Both terms are also used to refer definitely to consocies and associes respectively, but the context is usually decisive.

The basic correlations of communities may be illustrated by the following diagram (fig. 2):

CLIMAX FORMATION.

society - consociation - association - ecotone - association - consociation - society

↑ ↑

socies - consocies - associes - subclimax - associes - consocies - socies

(Prisere)		(Subsere)
↑	↑	
mictium.	mictium.	
↑	↑	
associes.	associes.	
↑	↑	
associes.	associes.	
↑	↑	
associes.	associes.	
↑	↑	
associes.	colony.	
↑	↑	
associes.	family.	
↑		
associes.		
↑		
colony.		
↑		
family.		

FIG. 11.—Diagram of the climax and seral communities of the formation.

Community structures.—In addition to the units themselves, associal and consocial communities show general structural features, such as zones, alternes, layers, and aspects. These are due primarily to the grouping or appearance of the subordinate communities with reference to a particular factor or factor-complex, and are of the greatest indicator value. The well-known zonation of the hydrosere in and about ponds is the best example of this. Each zone not only marks the general factor limits for its proper community, but also a distinctive step in the decrease of water-content and the increase of soil-air from the extreme conditions in the center. Such a series actually shows on the ground the "before-and-after" correlation of each stage typical of succession. Seral zones may be formed by consocies or associes; in their fullest expression the major zones are marked by associes within which occur minor zones constituted by the consocies in the order of their requirements. The zones of high mountains are essentially similar, though they have to do with climax associations and consociations. The same zonal structure recurs universally, wherever climax or séral communities are grouped about a center of excess or deficiency of some factor or group of factors. Zonation is sometimes obscured, especially in the dense vegetation of prairies (Plant Succession, 133), but it is rarely altogether absent, except in initial communities.

Alternes.—Alternes are due to the interruption of zonation through any cause whatsoever (Clements, 1916:115), but they are especially typical where disturbed or other successional areas are found. They are frequent

in climax areas wherever inequalities of surface structure and so forth occur. The term alternation is applied to two types of structure, one in which the same dominant or subdominant recurs from place to place, the other in which two or more alternate over the same area. The first kind is usually seral, the second is typical of associes or associations, and also of socies and societies. Recurring alternes are clear-cut indicators of the same set of conditions, and are of the greatest value. Striking examples are found in the burn alternes of aspen or lodgepole in the Rocky Mountains. Alternating dominants or subdominants are likewise indicators of their respective habitats. As indicators, they are naturally less sharply set off from the related dominants, but this is compensated by the evidence afforded of the degree of their equivalence.

Layers.—Layers are best known in forests and the term has usually been restricted to the subordinate communities in them (Hult, 1881; Clements, 1916:15). With the increasing study of root-systems and their competitive relations, it seems desirable to recognize root-layers as well as shoot-layers. Our knowledge of the former is still rudimentary, but it is possible that they are more general and significant than the well-known layers of woody communities. It is almost axiomatic that a layer of either type will have a double indicator value. It indicates the general equivalence with reference to the controlling factor of all the important species in it. Conversely, it denotes the dissimilarity of the adjacent layers and marks a certain stage in the progressive modification of the controlling factor from its point of maximum. Layers also serve to indicate the course of seral development, in that they are generally absent during the initial stages. They appear during the medial stages and usually reach a maximum in the subclimax or climax, often disappearing in woody communities as they become mature. As a consequence, the presence of several layers indicates more or less optimum conditions as to water or light or both.

Root-layers are regularly determined by water-content, though soil-air and perhaps solutes also must sometimes be taken into account. In saline soils they are due to differences in the salt-content acting through its effect upon water-content, except where the salts are chemically injurious. As to water-content, root layers may be a response to the physical distribution as determined by penetration and evaporation, or to the ecological consequences of competition. In the great majority of soils, both causes play a part (cf. Cannon, 1911; Weaver, 1919). Many communities show a striking correlation between the demands of the shoot and the root-position. This is often expressed in the corresponding development of root and shoot as well. It is best exemplified in the desert scrub, in which the tall shrubs are most deeply rooted, the undershrubs less deeply, the perennial herbs still less deeply, while the low annuals of the rainy season are rooted only in the first few inches.

The obvious relation of shoot-layers is to light, though water-content and humidity must sometimes be taken into account also. The best development of layers is found in well-lighted forests with a light intensity between 0.1 and 0.02. The midsummer values are rarely conclusive, however, as the layers tend to develop in the order of increasing height, with the result that each layer receives the maximum during its period of major activity. Each layer thus has two indicator values, one when it is uppermost and another when it

has been overtopped by the later layers. This naturally does not hold for the primary layer of trees or shrubs and for the highest layer of herbs which develops last. The practical value of shoot-layers as indicators is in connection with the natural reproduction of forests and the selection exerted by light upon the tree seedlings of a mixed forest, especially of conifers.

Aspects.—The character of a community changes with the season. This is best shown in prairie where the characteristic subdominants reach their maximum at different times, producing three or even four aspects, viz., prevernal, vernal, estival, and serotinal (Pound and Clements, 1900:140). Similar aspects occur in the herbaceous layers of forests. The number decreases with the altitude and latitude, so that arctic and alpine regions usually show but two, spring and summer. The indicator significance of aspects is partly a matter of the societies which characterize them, but they have a seasonal value as well. This lies in recording the advance of the season and in permitting the determination of departures from the normal rate. The correlation of this with the behavior of crop-plants and with all processes which deal with the renewal or rate of growth each year should have considerable practical value. Phenological lists suggest these values, but are too general and unrelated as a rule to be of much service (Lamb, 1915).

XIII. KINDS OF INDICATORS.

Basis of distinction.—Each plant or community serves as the immediate indicator of a factor or group of factors. As a consequence, it may also be employed to indicate the process or agency which causes or modifies the particular factor, as well as that in which the factor or habitat is involved. When the process is one set up or controlled by man, the plant likewise becomes an indicator of practice, and gives direct service in land classification, agriculture, grazing, and forestry. The relations of the plant or community to process and practice are direct corollaries of the basic principle that each is the best possible measure of the conditions under which it grows. Such measures merely require correlation with a particular process or practice to be of immediate service. This is the inevitable sequence, whether indicator values are the result of actual experience or the outcome of scientific investigation. In the latter case, the correlation is merely more detailed or more definite. Thus, while they all spring from the basic relation of plant or community to habitat, it appears desirable to distinguish indicators with respect to the use made of them. On this basis, they may be recognized as factor indicators, process indicators, or practice indicators. Furthermore, the development of the field of paleo-ecology makes it desirable to extend the application of indicator principles to the geological past. The sequence of indications is essentially identical, but the results must be inferred from present-day investigations, and hence it is desirable to speak of paleic indicators in this connection.

FACTOR INDICATORS.

Basis and kinds.—Every habitat is a complex in which the factors are almost inextricably interwoven. Each factor influences every other factor, and is in turn affected by it. This relation should never be lost sight of, since it is essential to the proper understanding of every factor indicator. Nevertheless, some factors are of such paramount importance in the habitat-complex that it is desirable to relate the plants to them directly. This is particularly true of the direct factors, water, light, temperature, solutes, and soil-oxygen. The indirect factors, soil, slope, exposure, wind, and altitude, can act only through these, but they too may be connected with plants as indicators, whenever they exercise a compelling effect upon a direct factor.

Each factor leaves a distinct impress upon a plant or community in proportion to its intensity and the plant's habitual requirements. The plant becomes an indicator of a particular factor to the more or less complete exclusion of others only when the factor exercises the paramount limiting effect. This is regularly the case when it is present in marked excess or deficiency, and hence a factor indicator usually denotes one extreme or the other, or a tendency toward it. Even in such cases, some at least of the other factors are concerned in producing the particular intensity of the limiting factor or are themselves affected by it. Consequently, each factor indicator not only denotes the controlling or limiting factor, but also a sequence of factors related to it either as causes or effects. A hydrophyte indicates deficient aeration as well as excessive water-content, while a xerophyte as a rule marks high

temperatures and low humidity as well as low water-content. In some instances, two or more factors appear to be equally important, and the plant indicates all of them. An excellent example of this is seen in alpine plants, where temperature, water-content, and humidity are of almost equal importance, and wind and pressure of much significance. The situation may be taken to represent the factor-complex, and such plants may be said to indicate high altitudes.

Quantitative sequences.—It has already been pointed out that practically every species has an optimum habitat, in which it exhibits its typical indicator value. Outside the optimum or habitual habitat, it has a narrow range in the direction of less favorable conditions for it, and a wider range in that of more favorable conditions. The mere presence of a species or even of a community can not be taken as evidence of its normal indicator value. Its actual value can be determined only by reference to the normal habitat as well as to the plants associated with it. It is this which makes dominance of the first importance in arriving at indicator results. A plant is dominant only within the range of essentially optimum conditions, and its control decreases in both directions, but most rapidly toward less favorable ones. The behavior of the individual plants is in close accord with these changes in abundance. The species has its most typical form where it is dominant, and changes in size and form usually furnish clear indications of departures from the optimum habitat toward either extreme. Subdominance follows the same rules and has similar values, though these are less striking than in the case of the dominants. In the tall-grass prairies, the societies often approximate the value of dominants, but in woodland and forest they are always strictly subordinate, and their indications serve only for a minute analysis of the general conditions of the forest.

In the present condition of quantitative studies, seral and topographic sequences must furnish the chief source of the indicator values of dominants and subdominants. This will probably always be true to a large degree, but the rapid growth of quantitative methods will afford a more detailed basis, and one which can be understood in terms of factors as well as of plants. In this connection, it must be recognized that a floristic census has slight value, and that accurate results can be obtained only by the use of exact methods which have dominance and sequence as their chief objectives. The floristic outlook upon vegetation is a survival of the early days of distributional plant-geography, and it must steadily decrease in importance as ecology becomes truly quantitative in method and result.

Climatic and edaphic indicators.—Every factor plays a part in the development of a community as well as in the control of its final condition. In the developmental habitats the local conditions, especially those of the soil, are paramount, while in climax ones the general climatic factors are controlling. The local or edaphic conditions find their expression in the seral dominants and subdominants, and the communities which they constitute. The widespread climatic conditions are reflected in the climax formation, associations, and societies. As a consequence, it frequently becomes desirable to speak of climatic and edaphic indicators. Certain factors, such as water and temperature, will be represented by both climatic and edaphic indicators. Others, such as light, solutes, soil oxygen, are primarily edaphic, while still others,

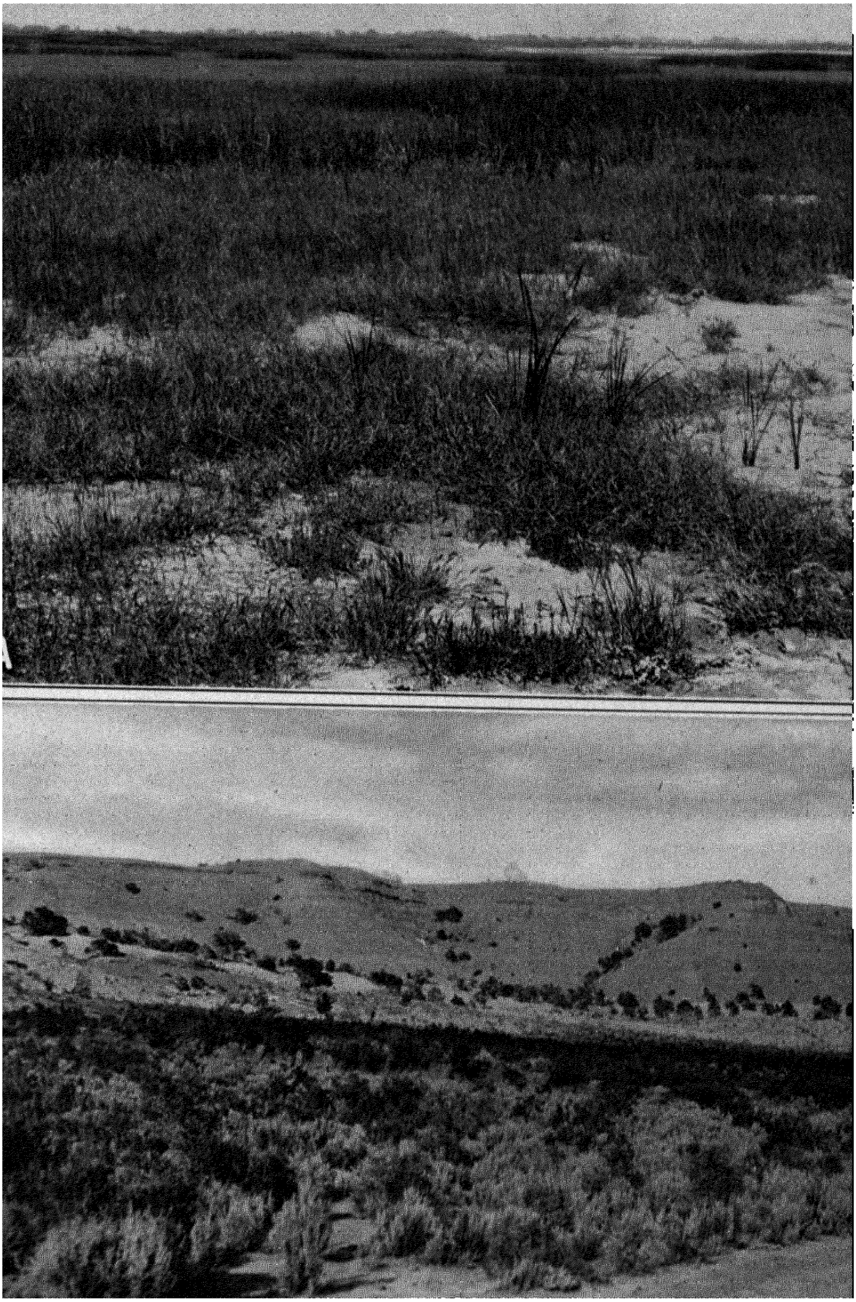
such as wind and pressure, may be either local or general. In the use of these terms for indicators, it must be clearly understood that the reference is to the nature and size of the area concerned, and not to the position of the factor in the soil or the air. In the sense employed here, climatic and edaphic indicators are synonymous with climax and seral ones, respectively, though the emphasis in the former case is upon the factors rather than the process of development.

Water indicators.—A detailed account of our present knowledge of the indicators of each factor is impossible within the limits of the present treatment. It must suffice to point out here the general relations of each factor to its plant and community indicators and to consider the most important and best understood of the latter in the chapters which have to do with climaxes and with practice indicators. The broader correlations of water and its indicators have already been touched upon in Chapter XII, and the following brief statement is intended primarily to emphasize some of the basic points involved and to suggest probable lines of advance in future work.

Water use will undoubtedly become the primary basis for interpreting the water-relations of plants, when the use of phytometric methods becomes general. Expressed in terms of transpiration per unit area and per gram of dry matter produced, this will furnish the first exact basis for the classification of plants on the basis of water. The application of such methods to native species will be a slow matter, however, especially under field conditions. Consequently, the indicator value of native plants for water must still rest largely upon determinations of water-content, humidity, evaporation, and the transpiration of standard plants, supplemented to some degree by studies of the form, structure, and growth of the plants themselves. Thus it becomes particularly important to refine the concept of water-content, since this exerts the basic control in water relations, and to render its expressions more definite and comparable (plate 27).

The general value of the echard for the various kinds of soils is now so well known that determinations of the holard are helpful in refining the values gained from sequences. This is particularly true when a single uniform soil is concerned, though even here account must be taken of differences at the various levels. The importance of the echard at the critical period has obscured the fact that it is the chresard which represents the amount of water available for the work of the plant, and that a very large number, if not the majority of species, probably never reach the echard during their lifetime. The water-response of such plants, and hence their indicator value, is concerned with the chresard. In the case of xerophytes and xeroid plants, including the crop plants of arid regions, the echard may be reached more than once during the growing season, or the plant may remain at that point for a considerable portion of the year. When the latter occurs, the plant bears a distinctive xerophytic impress, the intensity of which is apparently correlated with the length of the period of deficiency. The difficulty of making echard determinations in the field is such that in practice it is much more satisfactory to obtain this indirectly by means of the moisture-equivalent method of Briggs and Shantz (1912:56), and to express the seasonal chresard graphically, as has been done by Weaver (1917).

The lack of agreement between the results of the earlier investigators and



A. *Typha* alternes indicating pools in a salt-marsh, Goshen, California.
B. *Juniperus* indicating seepage lines in hills of Mancos shale, Cedar, Colorado.

those of Briggs and Shantz may be due in part to the more exact physical methods of the latter. So far as native plants are concerned, however, there seems to be no question that they vary considerably in their ability to obtain water from the same soil. This is obviously to be explained in part by the fact that the roots are not at the same level, and hence not in the same soil. But there are many cases in which certain species wilt before others, where the roots are interwoven in the same soil. As already mentioned, Dosdall (1919) has found that *Equisetum arvense* regularly wilts before *Helianthus annuus* and *Phaseolus vulgaris* when their roots are at the same depth in uniform soil. This agrees with results obtained in the field at the Alpine Laboratory with uniform gravelly soils, and indicates a considerable difference in the absorbing power of native species. This may be due to striking differences in the rate of transpiration or of the osmotic pressure of the root-hairs, or it may arise from differences in the extent and growth of the roots themselves. As Shull (1916:27) has suggested, it would appear less under moderate and uniform conditions, and it seems likewise that it would be less in evidence with crop plants and weeds which grow in fairly uniform root environments. It seems clear that this point must receive further investigation. Meanwhile, it is necessary to recognize that species of the same local group and habitat do wilt at different points, whatever the various causes may be.

In the endeavor to definitize the significance of water indicators, the primary division into hydrophytes, mesophytes, and xerophytes will still have value. In addition to the subdivision which Warming has already made of them, they will require still further analysis. This will become possible only with more exact study of the controlling factors, and especially of the actual water use. In fact, the precise meaning of any particular indicator will depend wholly upon the latter, and this will involve a readjustment of the relations of the main groups. Meanwhile, a keen appreciation of the need for more exact methods should not be allowed to obscure the fact that indicators of great practical value can still be made available by our present methods of ecological observation and instrumentation.

Light indicators.—In spite of the fact that small differences in light values are more readily detected by observation than with water-content, the recognition and use of plants as indicators of different light intensities are matters of recent development. The forester has long understood the general importance of light in the forest, and his tables of tolerance are an indirect recognition of indicator values. As long as he was chiefly interested in silviculture, however, tolerance was a matter of relative growth in the same or similar situations. The development of silvics as a phase of ecology directed attention more to the factors of the habitat, and led to the use of photometers for measuring light intensity. This has made possible the correlation of tables of tolerance with measured intensities and the use of the dominants concerned as direct indicators. Such work has merely been begun, however, and much quantitative study will be required before the general values of tables of tolerance can be made exact. Measurements of light intensity have been largely confined to forests, but it is clear that light values have considerable importance in other communities as well. This is especially true in woodland, scrub, and savannah, but it holds also for grassland, particularly the tall-grass prairies.

Two facts must be taken into account in correlating light indicators with measures of light intensity. One of these is the effect of variations in the composition or quality of the light. There can be no question that white light is modified in passing through the leaves of the forest canopy, the red and blue being absorbed to a larger degree than the green and yellow. In the case of conifers practically no light passes through the needles, and the light beneath them is white light, which has passed through the openings between the needles. In the case of broad-leaved forests, the amount of light entering between the leaves decreases with increasing density of the canopy, and that modified by transmission through the leaves becomes correspondingly more important. In all forests studied by the writer, the light has been essentially normal in composition, but there seems no good reason for questioning the results of Knuchel (1914; 1915:90) in beech forests especially. Even here, however, his tables and diagram show a somewhat uniform reduction in the different parts of the spectrum. Moreover, several facts indicate that the actual differences in quality in a beech forest are probably of little importance. Photosynthesis takes place almost wholly in the red and blue, which are more or less reduced. Furthermore, this function employs but a small part of the incident light, and a very serious disturbance of the normal composition would be necessary to affect it. Finally, reduction in intensity seems to have much greater influence than the change in quality. Forests of *Picea engelmanni* suppress the undergrowth even more completely than those of beech, in spite of the fact that the composition of the light is practically normal.

The significance of light indicators is also complicated by the influence of other factors. As already stated, this is the rule for all factors, but it is more marked in the case of light than of water. This is partly because light affects fewer functions directly, and partly because the modifying influence of water upon tolerance has been too much ignored (Plant Succession, 93). It is perfectly clear that the intimate interaction of water and light in competition, especially in forests, makes it necessary to take them both into account in determining tolerance as well as indicator values. This is true to a much smaller extent of nutrients and temperature, but these would have some influence wherever they tend to become limiting factors. Furthermore, there can be little question that light is usually the controlling factor in tolerance wherever the canopy is closed and that water plays a decisive part only when the light intensity is higher and evaporation and competition consequently greater. However, actual experimental studies of the respective rôles of the two factors, such as those of Fricke (1904), are needed for the various forest communities and the different groupings of dominants within them.

Tolerance has dealt almost wholly with the light relations of forest dominants (Zon and Graves, 1911). The latter are among the simplest and most direct of all light indicators, since they constitute actual experiments in planting, natural or otherwise. As indicators they have the same unique value as crop plants and, so far as practice is concerned, make the use of less direct indicators and of instruments more or less superfluous. In many cases, however, seedlings of a particular dominant or of all the related ones are absent from the forest floor, or the forest itself may be represented only by the undergrowth or certain elements of it. In such cases, the subdominant shrubs and herbs must be employed as indicators. The latter in particular

are often more sensitive than the trees themselves and hence furnish a more exact scale of indications. The widespread occurrence of certain herbaceous societies throughout one or more forest associations, or even formations, affords a striking opportunity for correlating the light relations for dominants associated under varying conditions as to other factors. The perennial herbs are of especial importance in this connection, as the effects of differing light intensities are clearly reflected in a variety of ways, in density, form, height, flowering, etc.

In definitizing the use of light indicators, it will be necessary to resort more and more to quantitative measurements of responses and factors. The most important responses in this connection are photosynthesis and growth. Both of these have certain values, and they will be more and more employed in combination, as complete and accurate results become necessary. At present, however, the determination of photosynthesis and its correlation with light is a much simpler and more exact process. As a consequence, the best determination of indicator values for light will continue to be initiated by close observation of general correspondences, which are first tested by means of measurements of intensity and then by studies of photosynthate production. It is probable, indeed, that this will give the real light indication without recourse to growth responses, but the latter will prove necessary to obtain the full indicator value for practical purposes.

Temperature indicators.—Temperature produces no clear-cut response in structure or grouping, and hence its indicators are not readily recognized by observation alone, as in the case of water and light. The most obvious response to it is growth, but this is affected so profoundly by other factors in nature that a primary correlation with temperature is always difficult and usually impossible. As a consequence of their striking distributional correlation with latitude and altitude, a number of endeavors have been made to classify plants with reference to temperature. The most suggestive are the classifications of A. de Candolle (1874) and Drude (1913:154). Both of these are based upon general climatic features, and take some account of water as well as temperature. While they have more or less interest, their ecological value is slight, owing to the almost complete lack of experimental and quantitative bases. Moreover, the usefulness of the groups is further reduced by such terms as "Etesial-Poikilotherme-Psychrochimenen."

The most notable attempt to correlate flora and fauna with temperature is that of Merriam (1890, 1894, 1898). The laws of temperature control of the geographic distribution of plants and animals are stated by him as follows:

"The northward distribution of terrestial animals and plants is governed by the sum of the positive temperatures for the entire season of growth and reproduction, and the southward distribution is governed by the mean temperature of a brief period during the hottest part of the year."

His well-known system of life-zones was established upon the basis afforded by these hypotheses. As indicated by his discussion of the Arctic, Hudsonian, and Canadian zones (1898:54), the life-zones appear to be actually based upon the outstanding vegetation zones of the continent, with temperature control as a more or less correlated principle. While Merriam's system has been of undoubted service in studies of floristics, its ecological value rests upon

the extent to which it has followed the natural vegetation zones and climaxes, and upon the correlation of these with crops. It can not be regarded as furnishing adequate proof of the paramount control of temperature in so far as plants are concerned at least. It possesses the disadvantages of every system erected upon a single factor, and emphasizes the basic truth that studies of causes must be grounded upon experiment, and not merely upon field observations and meteorologic data.

While there can be little or no question that every species has a climatic maximum and minimum of temperature, this is known experimentally for none of them. What is ordinarily observed in nature is, broadly speaking, an optimum to which the plant is more or less confined by the action of competition, water, and other factors. Theories of temperature control have generally failed to realize the unique importance of the period of germination and seedling establishment in determining the range and dominance of a particular species. There is sufficient experimental evidence in the case of a few dominants to suggest that many if not all of them can be extended beyond their present northern and southern, as well as their altitudinal limits, by the proper control of local conditions during the period of early ecesis. Moreover, when the part played by water in many of the effects supposed to be caused by temperature is adequately understood, it will be recognized that many of the so-called temperature responses must be ascribed to the combined action of the two.

In accordance with the rule, the impress of temperature should be most pronounced in climates where it is most extreme. These are arctic and alpine regions, and the tropics and subtropics. However, the influence of water is also pronounced in the first two, and over much of the other two. The dwarf shrubs and perennial herbs of alpine and arctic regions have long been regarded as undoubted responses to short seasons and low temperatures. But in the case of some alpine plants at least, it is certain that dwarfing is due as much or more to water than to temperature (Clements, 1907). It appears highly probably that this is true of the dwarfing of trees at timber-line also. In the latter case, the non-availability of the water-content is caused by freezing, and the dwarfing might well be regarded as due to both the direct and indirect action of temperature. A similar relation exists in tropical and subtropical deserts, where the actual impress is largely due to water. The latter is profoundly influenced by temperature, which appears to be in control of distribution to a considerable degree, especially in the case of succulents (Shreve, 1911, 1914).

If some weight be assigned to the indirect action of temperature, a considerable number of species may be regarded as temperature indicators. These are primarily alpine and arctic plants, and the succulents of hot desert regions. The trees and shrubs of the boreal tree limit and of timber-line on mountains are similar indicators, and this is true to some degree of those trees which become shrubs as they extend downward into the deserts of the Southwest. The absence of certain life-forms and species as a consequence of frost also constitutes a temperature indication of great importance. As a consequence of the gradual change of temperature with latitude and altitude, climax communities serve as the best of temperature indicators. They combine the responses of both life-form and species on such a large scale that there

can be little question of the paramount control of temperature where its extremes are concerned. Between the latter, climax dominants and communities must be regarded as primarily related to water, and hence treated as indicators of it. While these doubtless have relations to temperature which are susceptible of measurement, they are subordinate, and in our present incomplete knowledge can not be regarded as indications of it.

Indicators of solutes.—The term solute is used here to indicate any substance dissolved in the holard. It may be solid or gaseous, or even liquid. The best-known solutes are the mineral salts found in the soil, of which some are nutrients, others more or less inactive, and some actually deleterious to the plant. Of the gases dissolved in the holard, oxygen and carbon dioxid are the most important, but oxygen is the only one which bears a clear relation to indicator plants. In addition, there are the debatable toxic exudates and soil toxins, the existence of which is in doubt or the relation to the plant uncertain. Livingston, who has devoted much attention to this subject (1918: 93), states:

"Evidence that agricultural plants do actually excrete toxic substances into the soil is not very strong in any of this work, however. As to the manner in which these poison substances arise in the soil, no definite statements can yet be made, but they are surely not excreted *as such* from plant roots. There is physiological evidence, however, that such substances are given off by living roots when the latter are practically deprived of oxygen."

In so far as indicator plants are concerned, the effects ascribed to toxins are much better explained on the basis of an inadequate supply of oxygen (Clements, 1921).

The ordinary nutrient salts of the soil rarely leave a distinctive impress upon plants, owing to lack of concentration. When the concentration reaches a point where absorption is interfered with, the plant makes a definite physiological and structural response to the saline or alkaline conditions. The relation to lime and magnesia is less clear and the indicator impress less marked. In the case of deficient aeration, the response is clear, but its expression is often limited to physiological and histological features. Since all solutes act through water or in conjunction with it, their effects are often obscured by the responses to it. This is particularly true of saline indicators, which are merely xerophytes of a more or less peculiar type.

Saline indicators.—The term saline is preferred as the general term for all soil conditions in which soil salts occur in excess or a deleterious alkaline salt is present. In the West it is practically synonymous with the word alkali, and the two are employed interchangeably. Saline indicators are typical of sea-shores the world over, but their most striking development is found in the arid basins of the interior of continents, such as the Great Basin of North America. Practically all the work with them has been done in such regions, where the limits set by alkali to agricultural development are of the greatest importance. The outstanding studies in this field are those of Hilgard (1906) and Kearney (1914), and their respective associates. The work of Hilgard touched a large portion of the West, but dealt especially with California; that of Kearney and his associates was confined to the Tooele Valley in Utah, but it is applicable to the major part of the Great Basin. Both dealt specifically with the tolerance of the important dominants, but the work in Utah was

A. *Hordeum* plain and *Suaeda* hummocks indicating differences in salt-content, Great Salt Lake, Utah.

B. Communities of *Phleum-Equisetum* and of *Juncus-Heleocharis* marking differences in water-content and aeration, Sapinero, Colorado.

much more intensive, treating the plant communities in detail, and measuring the water-content and salt-content at different depths and in a wide variety of conditions. The indicator values of this classic study were completed by Shantz (Clements, 1916: 233), who brought out the successional relations of the various communities (plate 28, A).

Plants indicate alkali by their presence or absence. The positive indicators are the halophytes, which bear a distinctive xerophytic impress, caused primarily by the decreased chresard in the presence of an excess of salts. When the relation is chiefly one of concentration, the condition is known as "white alkali." This is due to the presence of sodium chloride, sodium sulphate, calcium sulphate, or other salts which possess no directly injurious action. Sodium carbonate produces "black alkali," which is directly deleterious to the plant, probably through corrosion of the tissues. The latter renders the soil useless agriculturally, while the former does not, except when present to an excessive degree. Since the three sodium salts often occur together, the plants of alkali soils serve chiefly as indicators of the total concentration, and the significance of the "black alkali" can be determined only by chemical analysis or crop test. Hilgard (1906: 535) regards the following species as indicators of irreclaimable land when they occur as dominants, unless the land is underdrained to remove the excess of salts: *Sporobolus airoides, Distichlis spicata, Spirostachys occidentalis, Salicornia* spp., *Dondia torreyana, D. suffrutescens, Sarcobatus vermiculatus, Frankenia grandifolia campestris,* and *Cressa truxillensis.* In the Tooele Valley the crop-producing powers of saline lands have been summarized by Kearney *et al.* (1914: 414) in the following:

Community indicators of crop production in saline lands.

Type of vegetation.	Is land capable of crop-production—	
	Without irrigation.	With irrigation.
Artemisia tridentata..	Yes	Yes ....
Kochia vestita	Precariously in years of rainfall above the normal........	Yes; if alkali can be removed.
Atriplex confertifolia.	Precariously; conditions rather more favorable than on Kochia land	Yes; after alkali is removed.
Sarcobatus-Atriplex ..	No	Yes; after alkali is removed.
Sporobolus-Distichilis .	Probably not.................	Possibly; with drainage.
Spirostachys-Salicornia.	No	No.

Lime indicators.—The original plan of giving a concise but complete account of the various views as to the effect of lime on native vegetation has necessarily been abandoned by reason of the limitations of space. Consequently, it must suffice to point out that the former views of the calciphily or calciphoby of various species are untenable, and that the effects usually ascribed to lime are either due to a complex of factors or to its indirect action. Schimper (1903: 94) has presented the best summary of the arguments which support the assumption that lime is a factor of primary importance, but even his account reveals the many weaknesses of the theory. The latter are clearly brought out in the following statement:

"External conditions, however, change with the area. In one area, the silica-form, in another the lime-form, is better adapted to local conditions, whilst in a third area both forms may be able to maintain themselves in the struggle for existence. Accordingly, one and the same species is caliphobous in the first area, calciphilous in the second, and indifferent in the third." (p. 104.)

One by one the "calciphile" and "calciphobe" species have been found or grown in the opposite conditions, until practically no obligate species remain. The present situation is well expressed by Warming (1909: 58):

"Recently it has been definitely established that the amount of lime in itself, in so far as it does not operate physically, can not be the cause of differences in the flora, for not only can calcicolous plants be cultivated in soil that is poor in lime, but silicolous plants, and even bog-mosses, which are regarded as pre-eminently calciphobous, can grow vigorously in pure lime-water if the aqueous solution be otherwise poor in dissolved salts. It has been overlooked that nearly all lime soils are rich in soluble mineral substances, and this wealth excludes plants belonging to poorer soils; beyond this the important physical characters of calcareous soil, compared with granite soil, come into play."

The century-old controversy over the significance of lime has been as unscientific as it has been useless. No ecologist questions the influence of both the chemical and physical properties of the soil, though there can still be much opportunity for disagreement as to their respective importance, where observation is the method relied upon. The general employment of quantitative methods and experiments in the field would long ago have assigned to lime its proper position. Naegeli (1865) was perhaps the first to point out that the response to lime was largely a matter of competition, and the validity of this explanation has been greatly increased by cultures showing the facultative nature of "calciphile" and "calciphobe" plants. His conclusions were based upon observational studies, however, and like all such work, can only suggest working hypotheses for critical field experiment. The following statement (Clements, 1913: 76) seems still an adequate summing-up of the lime problem:

"To one skeptical as to the influence of lime, the results of the Excursion were most interesting. One could not fail to be impressed with the abundant evidences of the distributional significance of lime, while he was struck by the fact that scarcely a single 'calciphilous' or 'calciphobous' plant could prove a clear title to the term, physiologically. It is useless to add a single line to the literary solution of this hoary problem, but the British experience serves to emphasize the conviction that nothing but physiological and competition studies in the field can hope to lead to a final solution."

In the western United States lime has nowhere been found to be a direct factor of importance. Neither observation nor experiment has disclosed any definite correlation with it, and hence no plants have been found which can be regarded as lime indicators. The plants of wet soils which have been considered to indicate the absence of lime are dealt with in the next section.

Aeration indicators.—The effects of wet and acid soils upon plant behavior have long constituted a puzzling problem. The leading rôle in such habitats as marshes and bogs has been assigned to various factors, such as acids, bog toxins, toxic exudates, the absence of lime, and the lack of oxygen. Probably

all of these are more or less concerned in the problem, with the exception of the supposed exudates, but the view held here is that the lack of oxygen is the cause, and the other conditions, consequences, or concomitants (Clements, 1916: 90; 1921). The presence of acids and bog toxins is regarded as the direct result of the activity of the roots and bog flora under deficient aeration (cf. Stoklasa and Ernest, 1909: 55; Livingston, 1918: 95). The absence of lime is apparently a concomitant of acid production, since the addition of lime to an acid soil either neutralizes the acid or affects the colloidal relations in such fashion as to make the soil agriculturally productive. It is significant, however, that lime is not the only substance that has this effect, since it is also produced by other materials which improve aeration. An acid soil is regarded as unfavorable to plant growth primarily because of the deficit in oxygen, and consequently also because of the poor development of the microorganisms that reconvert organic nitrogen into available form (plate 28, B).

The current assumption that bog water contains acids or toxins which are in themselves unfavorable to absorption seems disproved by the experiments of Bergman (1919). This investigator submerged pots containing plants of *Phaseolus* in bog water and tap water respectively until the tops were covered. In both the leaves wilted and turned yellow within 3 days. Both the bog water and tap water were then oxygenated night and morning, and by the following day the leaves had regained their normal turgor, and remained so for several days while oxygen was supplied. Similar results were obtained with *Geranium* and *Impatiens*. With the former, bubbling carbon dioxid through the water containing turgid plants produced wilting on the second day, and led to final chlorosis and fall of the leaves. When pots of *Impatiens* were submerged in water with and without *Philotria*, the ones remained turgid, while the others wilted within 3 days. Plants of *Coleus* and *Fuchsia* were grown in ordinary pots and in submerged ones, and the root pressure was found to be two or three times as great in the former. When the plants in the submerged pots were aerated by bubbling air, or by placing *Philotria* or *Spirogyra* in the water, the root pressure was nearly as great and as well maintained as in the normal conditions. Hydroid species, such as *Salix* sp., *Cyperus alternifolius*, and *Ranunculus sceleratus*, grew about equally well in bog water and tap water, whether aerated or not.

The studies of Hole and Singh (1914: 10) upon aeration in forest soils indicate that the lack of oxygen is a factor of greater importance and wider extent than has been supposed. The general summary of their results is as follows (101):

"1. The present experiments have confirmed the results previously obtained regarding the very injurious effect of bad aeration on the growth of Sal seedlings in the local forest soil.

"2. When water is long held in contact with this soil, which is the case under conditions of bad aeration, it becames heavily charged with carbon dioxid and impoverished as regards its supply of oxygen.

"3. The bad growth of Sal seedlings in this soil is correlated with an accumulation of carbon dioxid in the soil-solution and a low oxygen content, and this possibly explains the evil effects of bad aeration. Further work, however, is required to prove this and also to decide the relative importance of carbon dioxid and oxygen, respectively.

"4. Liming this soil, immediately before sowing, has an injurious effect upon Sal seedlings, and, during the rains, soil which has been thus limed appears to contain more carbon dioxid and less oxygen than the unlimed soil. It seems possible that this may be due to accelerated bacterial activity.

"5. As carbon dioxid is rapidly dissipated and a deficiency of oxygen made good under the ordinary conditions of water cultures, it is not easy to prove the effect of varying quantities of these gases on plants grown in cultures. For the same reason, artificial aeration of such cultures may not show any beneficial result.

"6. As Sal seedlings can be successfully grown in water cultures, the injurious effect of bad aeration is not due to water as such. This probably explains the fact that Sal can grow on the banks of the rivers or even of stagnant lakes, in which the water is kept well aerated by exposure to the air or by the presence of green aquatic plants."

The significance of aeration in field soils has been emphasized by Howard (1913: 7, 10):

"Important results have been obtained relating to water-logging and drainage, and it is suggested that these matters are of far greater importance than is generally supposed. Even partial water-logging has been shown to reduce the wheat crop 50 per cent. It is possible that the so-called indigo disease is the consequence of water-logging and a want of cultivation in a wet season, and that the best way of dealing with the situation is by improved drainage and by a more thorough aeration of the soil. I believe the damage done to land in Bihar by water-logging during the monsoon is not even dimly realized. Land can be harmed by water-logging when water does not lie on the surface for long periods and when water-logging would not even be suspected."

Plants may indicate good or bad aeration. The former are naturally of little importance as aeration indicators, since their impress is due to some other factor or factor-complex. Aeration indicators proper are correlated with a deficiency of soil-oxygen, and are naturally confined to wet soils and water, owing to the inverse relation existing between the amount of water and of oxygen. They may be conveniently arranged in four groups, based upon the kind of response to deficient aeration. In the first two, the species have developed adaptations which enable them to live so successfully in swamps and bogs that the habit is now obligate for the majority of them. The species of swamps regularly possess a special aerating system of air-passages and diaphragms, often supplemented by superficial roots and a marked movement of the transpiration stream. Such indicators are found typically in *Equisetum, Juncus, Heleocharis, Scirpus, Alisma, Sagittaria, Sparganium*, etc. Air-passages also occur in some bog-plants, but they are little or not at all developed in the shrubby species, such as *Vaccinium, Ledum, Andromeda, Kalmia, Empetrum*, etc. In most of these, the aeration devices are subordinate to those designed to conserve the water-supply during drought, especially in winter (Gates, 1914). Coville (1911, 1913) has emphasized the importance of good aeration for the successful culture of the blueberry, pointing out that this is secured in nature by the superficial roots as well as by their position in hummocks. It is probable also that mycorhiza plays an important rôle, partly in increasing the available nitrogen, and partly also perhaps in directly compensating for the deficit in oxygen.

The other two groups of aeration indicators consist of plants which grow normally in well-aerated soil. Hence they lack special adaptations for aeration, and consequently serve to indicate a lack of oxygen by their growth or distribution. Those which are somewhat tolerant of water-logged and poorly aerated soils respond to reduced oxygen content by decreased growth and reproduction. Intolerant species drop out, and their reduced number or absence serves as an indicator of conditions. Field studies of aeration or acidity have been few in the region concerned here. The most important is that of Sampson (1912: 51) in the Wallowa Mountains of northeastern Oregon.

Indicators of factor-complexes.—While indicators are concerned most immediately with direct factors, they are also definitely related to the indirect ones. Since the water-content is profoundly influenced by the nature of the soil, water indicators often serve as indicators of soil also. In practice, the character of the soil is more readily recognized than the amount of water in it, and the indicators of good soil represent not merely an adequate water-content and air-content, but a proper supply of nutrients as well. Slope or exposure and altitude are similar factor-complexes, in which the relation of the indicator to the complex is often clearer than it is to any one of the factors in it. In all of these, however, it is understood that the correlation is with one or two limiting factors, which are controlled or modified by soil, exposure, or altitude.

Soil indicators.—Since the soil is the seat of water-content, salts, oxygen, and acids, as well as of numberless organisms, it may be related to the indicators of any of these. This is the case in ordinary practice, and plants are spoken of as indicators of moist soil, alkaline or acid soil, as the case may be. In the stricter sense, indicators refer to the soil as defined by its physical properties, though this necessarily includes water-content. On this basis, plants may be indicators of sand, clay, loam, or humus soils. When their growth and distribution are taken into account, they may serve to indicate even finer divisions of each of these types. In such cases, however, local variations in water-content are often more potent than soil texture, and correlation with one does not necessarily mean correlation with the other. Since the physical character of the soil is of primary importance in determining the echard, soil indicators may be used to distinguish high and low echard. The plants of clay and humus soils are indicators of the one, those of gravelly and sandy soils of the other. In humid regions this distinction is of little importance, except possibly in relation to drainage, but in arid climates or during seasons of drought it is frequently a vital matter. This has been emphasized by Shantz (1911: 87) in his indicator studies in eastern Colorado:

"Many of the older settlers in eastern Colorado have moved from short-grass onto wire-grass land, or even bunch-grass land, where they claim there is much less likelihood of crop failure; but the newcomer in the region or the speculator almost invariably chooses the hard or short-grass land because it is darker in color, and looks more like the soil he has been accustomed to farm successfully in the East."

Slope-exposure indicators.—While slope and exposure are regarded as distinct topographic features, they are so intimately combined on every

hill and mountain that their separation is undesirable, so far as indicators are concerned at least. Both modify the direct factors, water-content, humidity, light, and temperature, and through them nearly all other factors of the habitat. Exposure is of the most immediate importance, as it determines the exposition toward the sun or away from it, but is itself determined in large measure by the angle of slope. Exposure directly affects the temperature and humidity, and through them the water-content, and consequently the nutrients and aeration. A northerly exposure also reduces the amount of direct sunlight, but this is perhaps felt only in transpiration. An increase in the angle of slope has a marked effect in increasing the runoff and correspondingly reducing the water-content. Perhaps its most significant result lies in emphasizing the effects of exposure toward or away from the sun. Together the two increase temperature and evaporation, and decrease humidity and water-content on all southerly exposures, while they have just the opposite effect on northerly ones. In arid regions, the effects upon plants are often most pronounced. Succession moves much more rapidly and the climax is reached much sooner on the north side, with the result that the communities often differ greatly on the north and south slopes of the same hill. Growth usually begins earlier on south slopes, but the plants are taller and denser on north ones. The indicator differences deal with the presence or absence of various species and the corresponding communities, and with the growth and abundance of the individuals. Such indications are related primarily to water-content and evaporation, though temperature plays a direct rôle of some consequence.

Alternation in vegetation is largely a matter of slope-exposure (Clements, 1904: 165; 1905: 285; 1907: 289). Much attention has been given to the alternation of dominants and subdominants on different slopes in the rolling prairies of Nebraska and the mountains of Colorado. Shantz (1906: 25) has shown the variation in temperature and light intensity during the day for different slopes in the short-grass association at Colorado Springs. Weaver (1917: 43; 1919) has made a detailed study of the evaporation, water-content, and temperatures of northeast and southwest slopes in the Palouse region of Washington and adjacent Idaho. All the factors agree in showing that the southerly slopes are much more xerophytic, and readily explain the absence of a large number of species, or their greater abundance on the northerly slopes. Spalding (1909: 43) studied the occurrence of species on two opposite slopes in the desert scrub at Tucson. He found that they had 15 perennial species in common, while the northeast slope had 24 not found on the southwest, and the latter 9 not present on the other. Shreve (1915: 97, 61) has given a detailed account of the differences in the vegetation of the Santa Catalina Mountains due to slope-exposure, and in the factors concerned.

Altitude indicators.—Altitude is not so much an edaphic factor-complex as the expression of a specialized climate, of which elevation above the sea-level is the remote cause. This expression occurs in some degree at all altitudes, but its accumulation becomes most striking at the higher ones and especially above timber-line. Because of the close relation between altitude and latitude, the actual level of a particular effect, such as timber-line, varies from sea-level at the northern tree-limit to 12,000 feet or more in the southern Rocky Mountains. As is well known, the direct effect of increased elevation

is seen in reduced pressure and a correspondingly rarefied atmosphere, which is the primary cause of most of the changes. The factor most affected is temperature, the rays passing readily through the rarer air during the day, while for the same reason radiation is very rapid at night. As a consequence, the soil and the air immediately above it may become very warm on a sunny day and then drop to freezing at night. On Pike's Peak the surface of the soil may show a temperature of 140° F., while in the air 5 feet above, the temperature is but 70° F. Probably still more important is the shortness of the growing season. The frostless season is nearly 5 months long at Colorado Springs (6,000 feet), while on the top of Pike's Peak (14,100 feet) frost occurs frequently throughout the summer. The light changes little in quality or intensity with the altitude in the Rocky Mountain region generally, though this may be due to low humidity. The relative humidity increases, but evaporation and transpiration are greater at higher elevations, owing to reduced pressure, wind, etc. The annual precipitation rises steadily with altitude, and an increasing amount of it occurs as snow. The excessive snowfall of subalpine and alpine regions accounts for many of their characteristic features and explains the generally high water-content. Winds are usually prevailing and forceful, and have both a direct and indirect effect in the dwarfing of trees at timber-line. The indicator values associated with high altitudes are primarily due to temperature or water, or usually to both acting together. With the exception of the wind and snow forms of trees and shrubs, all alpine and subalpine indicators are related to these factors in the region concerned.

The sharp change of climate with altitude produces a corresponding sequence of climaxes, which serve as the most outstanding of indicators. These are considered in more or less detail in the following chapter. In addition, the majority of montane and alpine species have rather definite lower and upper limits, and may be used as indicators of altitude, though a correction is necessary for those of wide range in latitude. Cockerell (1906: 861) has made an analysis of the alpine species of Colorado, based upon Rydberg's Flora of Colorado (1906), which brings out their altitudinal relations clearly, and makes it possible to use many of them as altitude indicators for the central Rocky Mountains.

Organism indicators.—The many basic relations between plants and animals make it clear why the plants often serve as definite indicators of animals. Animals may also act as indicators of plants, but to a less degree and in a less definite manner. In addition, plants regularly serve as indicators of such other plants as bear a distinct nutritional relation to them. This is particularly true of the fungi and bacteria, of which one of the most striking indicator relations, the fairy ring, has already been discussed (p. 218). The use of plants as indicators of animals is based upon the relation of food, shelter, disturbance, or pollination. In all of these the indications may be very definite, a certain plant or community denoting a particular animal, but as a rule the relation is necessarily more general. In some cases, moreover, the relation may be concomitant rather than causal, as in the case of the alpine conies and marmots, where the control seems to be rather one of climate than of the alpine plants upon which they feed. Furthermore, the indicator relation varies from region to region with the range of local occurrence of the species concerned. A striking example of this occurs in the relation of

the kangaroo rat (*Dipodomys deserti*) to the shrubs about which it makes its mounds. In the savannahs of the desert plains it occupies every clump of *Celtis pallida* as its first choice. In the usual desert mixtures of *Larrea* and *Prosopis* where *Celtis* is absent, the preference is almost exclusively for *Prosopis,* but when the latter is lacking or has been destroyed by the rats, the mounds are made about *Larrea.* In portions of the Colorado Desert, mounds of remarkable size are built about *Dalea spinosa,* and both *Prosopis* and *Larrea* are practically ignored. Throughout the desert scrub, one or the other of these four genera will be the indicator, depending upon their grouping.

Food and shelter relations are naturally often combined in the same community. When they are found in the same species, the indicator value of the latter is distinctive. This is not infrequent for mammals and birds, as in the case of *Neotoma* and *Yucca* or *Opuntia* in their respective communities, but it is best seen in the case of insects. The classic example is afforded by *Yucca* and *Pronuba,* but *Xyloscopa, Megachile,* and other genera of pollinators furnish similar instances, while the host-plants of gall-producing insects exhibit a like relation. Such examples are naturally rare among birds, but a close relation exists in some cases. Taylor (1912: 414) has called attention to this in the case of *Artemisia tridentata* and the sage-thrasher, *Oreoscoptes montanus,* and it occurs also between the cylindric opuntias and the cactus wren, *Heleodytes brunneicapillus,* as well as between the giant cactus, *Cereus giganteus,* and the gilded flicker, *Colaptes chrysoides.*

The indicator relations between plants and animals arising out of the disturbances caused by the latter are numerous, and play a large part in the study of secondary succession. Among the striking examples are ant-hills, rodent burrows, prairie-dog towns, and beaver dams. The indicators of this type are considered further in the section on paleic indicators.

PROCESS INDICATORS.

Nature.—Process indicators comprise those plants and communities which indicate definite processes in the habitat. Such processes may be natural, as when they are topographic or climatic, or artificial, when they are the result of disturbances due to man. Such a distinction is convenient rather than essential, since there is no real difference in the overgrazing due to a herd of bison and that caused by a herd of cattle, or in disturbances of the soil produced by primitive or civilized man. The latter, however, does cause disturbances in vastly greater number and on a much greater scale, with the result that the majority of process indicators ordinarily encountered are related to his activities. While the two have much in common, the more vital distinction is based upon the nature of the area, and the vegetational development which results (Plant Succession, 33, 60). Primary areas are represented by water-bodies, rock, dune-sand, etc., in which extreme conditions prevail, and a long line of development occurs. Secondary areas are due to disturbance by man or animals, or to superficial erosion or deposition. The conditions are usually much less extreme for the initial invaders, and the development is correspondingly short and simple. Both are alike, however, in that the successional development progresses by more or less well-marked stages, in which there is a definite relation between the dominants and the

factors. Each stage or associes thus serves as a community indicator of the conditions of the habitat, each consocies as an indicator of smaller habitat differences, and each socies of still finer differences.

Kinds.—Process indicators are grouped primarily upon the nature of the process itself. They are all indicators of the successional process in vegetation, and hence this relation is taken for granted. The great majority of them are concerned with unit successions or seres related to physiographic processes or disturbances, but many of them have to do with climatic processes or cycles, as found in potential succession, and in coseres and cliseres. Hence it is desirable to distinguish the indicators of primary processes, such as climatic and physiographic cycles, and those of secondary processes such as superficial disturbances which result in denudation merely, whether produced by man or other agencies. The major secondary processes are fire, lumbering, cultivation, grazing, engineering operations which involve cutting or filling, irrigation, drainage, and superficial erosion and deposition due to natural agencies. These are all alike in that they initiate secondary seres, but they differ sufficiently in detail to be characterized by more or less distinctive indicators. This is so true of some that it is possible to distinguish different kinds of cultivation, grazing, etc., by means of their indicators.

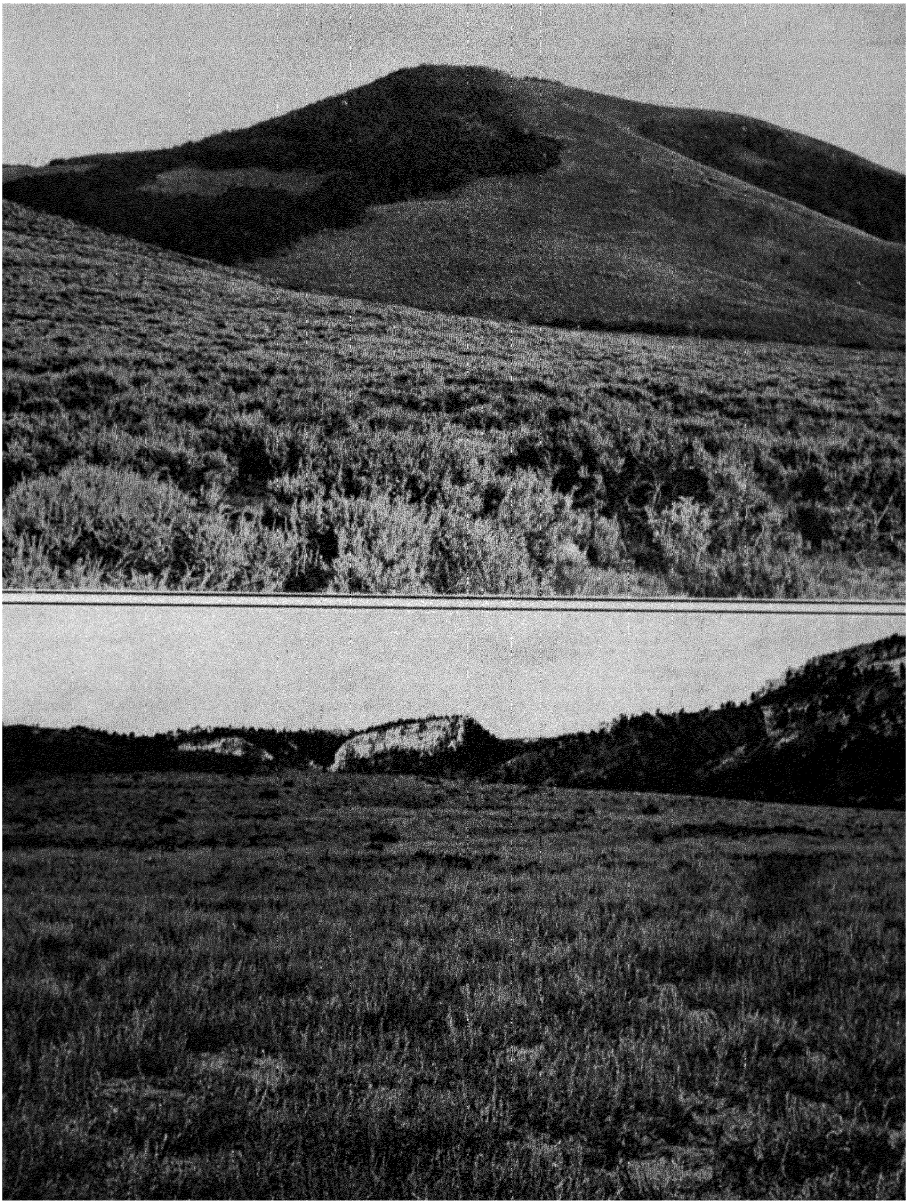
Process indicators serve not only to denote the kind of process, as well as certain variations in it, but they can also be used to approximate the time of origin and the rate of movement. This is the natural outcome of the sequence of stages in sere and habitat which marks succession. Moreover, they possess the further advantage peculiar to all successional dominants of indicating communities and conditions which have preceded, as well as those which are to follow, including the final climax. As already indicated, this is often of the greatest practical value in enabling one to restore an earlier condition or community, to hasten a later one, or to hold the succession in the stage desired. Accurate determinations of the rate of progress can be made only by the use of permanent quadrats, but it can often be closely approximated, in woody communities especially, by ascertaining the age of the dominants in relation to the life-history.

Fire indicators.—While fire has some points in common with other agencies which cause denudation, it differs especially in its action upon the surface soil and in the more or less complete destruction of plants and germules, as well as in the fact that the soil is not actually disturbed. These differences are reflected in the large number of indicators either peculiar to it or more typical of it than of other processes. Certain vegetation-forms appear to owe their character or at least their dominance to fire. This is particularly true of scrub, where the form and consequently the dominance are due to the root-sprouts produced after fire. This relation is practically universal in the Coastal chaparral, and explains the greater massiveness of this association in comparison with the other scrub communities. It is general in the Petran chaparral and the desert scrub, and is poorly developed only in the Basin sagebrush. The response to fire is typical of the subclimax chaparral in California and Oregon, as well as of that which occurs in the prairies of the Middle West. The bush or scrub type is a characteristic fire indicator in forest climaxes the world over, and throughout the northern hemisphere it often consists of the same genera and even species (plate 29, A).

Fire has played a similar rôle in making certain genera and species of trees almost universal indicators of its action. The best known examples are found in *Populus* and *Betula*. *Populus tremuloides* and *Betula papyrifera* are the characteristic indicators of fire in forest communities throughout boreal North America, as well as in many mountain regions. They owe this to their ability to form root-sprouts, and the trees often or regularly consist of several stems in consequence. In the Old World, corresponding species of the same genera play a similar part. A second striking group of indicators is found among the conifers, and especially the pines. The latter are characterized by cones which may remain closed upon the branches for many years, but open readily after fire, thus furnishing a large number of seeds for immediate ecesis. Three important species of this type occur in western North America, namely, lodgepole pine, *Pinus contorta,* jack pine, *P. divaricata,* and knobcone pine, *P. attenuata.* These are all typical fire trees, and form subclimaxes of great extent and duration in areas frequently swept by fire (Clements, 1910). In the Coast forest, *Larix occidentalis* and *Pseudotsuga mucronata* likewise owe their dominance in large measure to fire, though for reasons partly connected with their intolerance.

Among herbaceous plants the number of fire indicators is legion. A large number of these are annuals and biennials, but some of the most widespread are perennials, such as *Epilobium spicatum* and *Pteris aquilina.* They are not restricted to flowering plants, but are represented by *Pyronema confluens* among the fungi, *Marchantia polymorpha* among the liverworts, and *Bryum argenteum* and *Funaria hygrometrica* among the mosses. The most typical fire-grass is *Agrostis hiemalis,* while among the composites, *Anaphalis margaritacea, Achillea millefolium, Arnica cordifolia, Erigeron acris,* and species of *Carduus, Senecio,* and *Solidago* are especially important. In severe burns, the germules may be largely destroyed, and the resulting subsere shows distinct stages of which *Agrostis hiemalis* is the first community and *Epilobium* the second. Very often, however, the dominants of the various stages appear during the first two years, and the successional movement consists chiefly of the successive dominance of annuals, biennials, perennials, bushes, and trees, as they replace or overtop each other. Many of the herbs and bushes persist as layers if the shade permits, suggesting that they were originally derived from such. In most cases, their continued persistence as societies is connected with occasional ground fires. In such instances, the evidence furnished by their presence can be checked by means of fire-scars, the age of burned seedlings, and the presence of charcoal in the soil.

Lumbering indicators.—As a general rule, the indicators of lumbering operations are of much less importance than those of fire. This is due to the fact that the direct evidence afforded by stumps and relict trees is altogether conclusive, and that furnished by the herbs and shrubs is superfluous. In spite of this, there are not infrequent cases where the clearing has been so complete that the usual woody relicts are absent. Many of these are complicated by fire or cultivation, and some by both. However, in the midst of virgin forest, clearings occur in which the evidence as to the agent must be sought from the species in possession. In all clearings due to the ax, whether the direct evidence is still available or not, many of the dominants are the same as in burns. The chief difference in the two communities lies in the



A. Aspen indicating an early fire, and sagebrush alternes a recent one, Strawberry Cañon, Utah.

B. *Artemisia frigida* indicating an old fallow field, Warbonnet Cañon, Pine Ridge, Nebraska.

greater selection exerted by fire, with the result that the dominants are fewer in number and more controlling. For the same region, the major dominants are the same for both, particularly where fire has followed lumbering, as has been the rule.

Cultivation indicators.—As suggested previously, these might well be called indexes rather than indicators, since they are the consequence of cultivation instead of an indication of its possibility. The number of such indicators is very large and they vary from one climax to another in accordance with the flora. Many of them are introduced weeds, but the majority are subruderal species derived from the adjacent vegetation. The relative importance of the two elements varies greatly, but the introduced species decrease rapidly in number toward the interior as well as upward into mountain ranges. For a number of reasons, the prairies and plains exhibit the largest number of cultivation indicators, but they occur in all climaxes with the exception of the alpine meadow.

Especial attention has been paid to the subsere originating in fallow and abandoned fields, and on timber claims throughout the grassland climax. In the more arid portions of this vast region, there have been several waves of settlement, coinciding more or less closely with the wet phases of the sunspot cycle. These waves have receded during the drought phases of the early seventies, the early nineties, and of 1916-1918. However, the recession has been less each time, owing largely to better methods of tillage and to the diversification of crops. In the drought of 1893-1895, the Niobrara region of northeastern Nebraska was nearly depopulated, where to-day there exists an assured agricultural practice. As a consequence, also, the belt of abandoned fields and farms has moved westward, and the indicators have changed to correspond. Many of them occur over much of the region, however, and these are still those of greatest importance and almost universal occurrence. A large number are annuals, and the pioneers are all annual or biennial. As is typical of weeds and subruderals, they occur in dense stands of a single dominant, or a mixture of but two or three major dominants (plate 29, B).

The widespread dominants of the fallow fields of the prairies and plains are *Salsola* and *Helianthus*, the latter represented by *H. annuus* in the eastern portion, and *H. petiolaris* in the western. Both genera occur from Montana to Texas, but are more abundant southward. *Erigeron canadensis* is perhaps next in importance in fields, while *Grindelia*, *Gutierrezia*, and *Artemisia frigida*, though abundant, are of still greater importance in pastures. *Coreopsis tinctoria* and *Polygonum pennsylvanicum* are typical of moister fields in the eastern half, while *Anogra albicaulis*, *Oenothera rhombipetala*, *Eriogonum annuum*, and *Cycloloma platyphyllum* characterize fallow areas with more or less sandy soil, especially in the West. Other indicators of common occurrence are *Euphorbia marginata*, *E. geyeri*, *Ambrosia artemisifolia*, *Iva xanthifolia*, *Chenopodium album*, *Panicum capillare*, *Eragrostis pectinacea*, *Cenchrus tribuloides*, etc. A similar wealth of indicators of fallow or abandoned fields is found in California. *Eschscholtzia californica* is by far the most striking of these, though it is less widely distributed than *Amsinckia intermedia*, *Eremocarpus setigerus*, *Sisymbrium altissimum*, *Rhaphanus sativus*, *Brassica nigra*, *Bromus maximus*, etc.

Grazing indicators.—Like the species which indicate cultivation, grazing indicators mark disturbance in varying degree. It is likewise necessary to distinguish such indicators or indexes from those which denote the kind of grazing possible or desirable, and the carrying capacity as measured by number of animals. The latter are among the most direct of practice indicators, and might well be taken for granted, if their value did not change critically from one community to another, or in different portions of the same community. There is much less difference in the nutritive value of the ordinary grass dominants, for example, than in their palatability, but the latter varies greatly with the choice possible.

A considerable number of cultivation indicators are also indicators of overgrazing. This is explained by their common relation to disturbance. In the case of cultivation, the disturbance is much greater and usually operates in a shorter time. The disturbance produced by overgrazing is gradual and accumulative, and requires several years or more to attain definite expression. In the case of breaking and tilling in a new region on the plains, the original vegetation is completely or mostly destroyed, and a distinct subsere beginning with annuals is initiated. On the other hand, overgrazing changes the competition relations between the dominants as its primary effect, and the actual disturbance of the soil is usually secondary. The grasses and herbs that are not eaten gradually secure an advantage over the others, and correspondingly increase in dominance or importance. In most cases, they are already present in the community, but where they are not, their invasion from roadsides or other disturbed places into the trampled soil is a simple matter. There are in consequence two general types of indicators of overgrazing, *i. e.*, those due primarily to the fact that they are not eaten, and those which invade because of disturbance. There is naturally no hard-and-fast line between them, as is shown in the detailed discussion in Chapter XV.

As a consequence of the difference in the successional process, the indicators of overgrazing resemble those of old fallow fields, and there are instances in which careful scrutiny is needed to distinguish the initial cause. However, when trampling has destroyed the control of the dominants and greatly disturbed the surface soil, as happens frequently in sandy areas, a subsere beginning with annuals results. Throughout the grassland climax, there occur three overgrazing indicators which outrank all others in importance. These are *Gutierrezia sarothrae, Aristida purpurea,* and *Artemisia frigida.* There are many others of great significance, especially among the species of *Grindelia, Opuntia, Psoralea, Petalostemon, Verbena, Vernonia, Euphorbia, Carduus, Solidago,* etc., which are discussed in Chapter XV.

Indicators of irrigation and drainage.—These are related in that they are connected primarily with a decisive disturbance in the water relations, though they are more or less opposite in nature. Plants which register the effects of irrigation are numerous, and are to be found along every irrigation ditch and field. Those which indicate the possibility or desirability of irrigation are less definite and have received much less attention. Many of them are of great importance in denoting good soils of sufficient depth, *e. g., Artemisia, Prosopis,* etc., or sufficiently free from alkali, *e. g., Artemisia, Atriplex conescens,* etc. The disturbance of the soil in constructing irrigation canals and ditches, coupled with the abundant water supply, has permitted the development of

a large and varied plant population along them. This is composed largely of the weeds of cultivated fields and roadsides, but it also contains many subruderals developed from the natural communities. Macbride (1916) has made an interesting study of the successional changes which occur under irrigation, and his results serve to indicate the general indicator value of the dominants.

Plant communities serve as excellent indicators of the need of drainage, as well as of its progress and success. The need for drainage is clearly indicated by the presence of any one of the stages of the hydrosere or oxysere. The latter also indicates the necessity of liming the soil, or employing some other method of securing aeration and neutralization. Drainage hastens the movement and reaction of the succession in swamps and bogs, and the later seral stages clearly indicate when the successive points have been reached at which the area can be used for grazing, forestation, or crop production. However, in extensive drainage operations, the areas concerned are put into commission so rapidly that the natural communities are destroyed.

Construction indicators.—Practically all engineering and other construction operations in nature disturb the soil, often in a most striking fashion. The most common and important are the building of roads and the construction of railways and canals. The construction of buildings and similar operations belong in the same category, but the effects are usually masked by the subsequent activities of man. The general relation of engineering operations to succession and hence to indicators is best exemplified in the case of a railway cut and fill. In addition to the cut and the corresponding fill, there is often a dump of new earth on each side of the cut. These three secondary areas for succession have much in common, but the loose soil of the dump and the fill is invaded much more rapidly than the firm soil of the sloping sides of the cut. This difference is even more striking when the track runs through a level stretch and the bed is built up from soil scraped out from both sides. The moist depressions are readily invaded by the more mobile or vigorous species of the original community. The bed is not only more xerophytic, but also is disturbed from time to time. Moreover, invasion proceeds along it more readily than into it across the depressions which separate it from the native community. As a consequence, the bed remains more or less permanently in the early stages of succession, which consist of annual and perennial weeds, some of which are derived from the native population. The depressions, on the other hand, pass more or less rapidly through the usual stages to the climax, unless the sere is kept in the subclimax by burning or cutting. Their indicators are often of the most exceptional value in regions where the native vegetation has been greatly modified or largely destroyed.

Roads resemble railways in their general relation to succession and indicators. This is particularly true of highways in which cutting and filling, though less extensive, are as frequent as in the case of railroads. Roadsides usually show a typical zonation from the bare trackway to the natural community on either side (Clements, 1897: 968). The sequence of zones summarizes the successional movement, and the latter is shown in especial detail when there are many parallel roads of different ages (Shantz, 1917: 19). In addition to indicating the disturbance caused by roads, plants may be used as indicators in connection with road-building and even in traveling. The correlation between certain communities and good roads is as striking as it is

gratifying, and in actual travel it is often a matter of much importance to be able to determine the character of the road from the vegetation which stretches for many miles ahead. During the constant field travel of the past five summers, many communities have been recognized to have some value for road construction as well as travel, but there are a few of the greatest importance and the widest extent. Throughout the mixed prairies, *Stipa* generally indicates good upland roads, *Agropyrum,* poor lowland ones, while the presence of short-grass on the hills and ridges usually means a road made rough by the matted roots of *Carex.* In the sagebrush climax, sagebrush, *Artemisia tridentata,* indicates excellent natural roads, *Atriplex confertifolia,* much poorer ones, and *Atriplex nuttallii* and *A. corrugata,* very poor ones. Throughout the desert scrub, *Larrea* is an index of good roads, *Prosopis* of poorer ones, and the saline subclimax of the very poorest, except where the presence of sand makes some improvement.

Physiographic indicators.—Plant communities owe their significance as indicators of physiography or physiographic processes to the influence of the latter upon the direct factors, especially water and solutes. It is clear that the indicators of factor-complexes, such as slope-exposure and altitude, have a distinct physiographic correlation also. However, the basic relation between physiography and indicators is through such processes as erosion and deposition which directly control the soil and its water-content. Since physiographic processes are the universal causes of primary bare areas, their indicators occur in successional communities that mark the progressive change of the area from the initial condition to one of relative stability. As has been emphasized elsewhere (Plant Succession, 35), causes other than physiography may produce similar bare areas and initiate the same sere, the successional movement being due to the reaction of the communities alone, or to this and physiographic processes working together. In the great majority of primary areas, however, physiographic causes or processes are so important or controlling that the seral indicators are readily correlated with them and their changes.

The most outstanding and best-known series of indicator communities of physiographic processes is that of ponds and lakes. In these, physiography is normally the initial cause of the body of water, and deposition the process which controls or promotes the seral movement. The primary stages of the process are marked by the well-known associes of submerged plants, floating plants, reed-swamp, and grassland, or scrub. Pearsall (1917: 189) has recently pointed out that still other associes should be recognized, and these would serve as indicators of somewhat smaller changes. Finally, each consocies indicates a more or less definite set of conditions within the associal stage. The succession in dunes, sandhills, and blowouts is almost equally well known. In these the physiographic processes are very active, and the indicators of the different degrees of reaction or stabilization well-marked (Cowles, 1899; Gleason, 1907; Pool, 1914). The indicators of sandhills, and of river and coastal dunes have received much attention during the studies of the past five years. The dominants and seral communities are identical or similar throughout the West, except along the Pacific Coast, where a very different flora is concerned. During the same period, a special study has been made of succession in Bad Lands, and this has permitted the correlation of a

large number of indicators with erosion and deposition, and the resulting differences in water-content and salt-content. Similar though less extensive investigations have been made of the indicators of saline bolsons and playas, and of the geyser and mud-volcano areas of Yellowstone Park. Finally, the seral indicators of cliffs, rock-fields, and gravel-slides have been worked out for the central Rocky Mountains in particular (Clements, 1905: 270; 1916: 225).

Climatic indicators.—The value of climax communities as climatic indicators has already been emphasized. Formation, association, consociation, and society are correlated with different climates or climatic subdivisions, and their general values as indicators are pointed out in the succeeding chapters. In addition to this, plants and communities have striking significance as indicators of climatic cycles and hence may become of great value in determining the proper practices in production for the arid and semi-arid regions of the West. The existence of such cycles has been demonstrated beyond a doubt by the work of Douglass (1909, 1914), Arctowski (1912), Huntington (1914), Kapteyn (1914), and Clements (1916). The relation of climatic cycles to succession and hence to indicators has been discussed at some length in "Plant Succession," and an extensive study of the relation of the 11-year cycle to grazing and dry-farming has been made during the drought of 1916-1918 (Clements, 1917, 1918). A complete summary of the relations between cycles of rainfall, sun-spots, and tree-growth has recently been made by Douglass (1919, 1927).

Trees and shrubs are the best indicators of minor climatic cycles by virtue of the annual record of growth in rings. It is also probable that height-growth furnishes a correlated record, but little study has as yet been made of the cyclic nature of the latter. It has been found that the height-growth and the reproduction of dominant grasses and halfshrubs, such as *Bouteloua, Agropyrum, Gutierrezia,* and *Isocoma,* show a close correspondence with the rainfall of the dry and wet phases of the sun-spot cycle. It is, moreover, a matter of general experience that the carrying capacity of the western ranges varies 100 per cent or more from wet periods to times of drought. Even more striking variations in the yield of field crops are shown for similar periods (Ball and Rothgeb, 1918: 49). Since wet phases usually offer the best conditions for germination and growth, and drought periods the poorest, the ecesis of dominants often affords striking indications of climatic phases. This is especially well seen in the ecotone between two adjacent communities such as grassland and scrub, woodland and sagebrush, or forest and grassland. In the majority of cases so far investigated in which a woody dominant is extending into another community of smaller water requirements, the annual rings indicate its establishment during the wet phase of the cycle.

The general significance of climatic cycles and of cycle indicators in practice is discussed in the next section. Their fundamental value in paleo-ecology is dealt with under paleic indicators at the close of the chapter.

PRACTICE INDICATORS.

Nature.—Practice indicators are those plants or communities which point out the possibility or desirability of a particular practice. This is the original as well as the general use of the word "indicator," and there are good reasons for restricting it to this sense, and designating the so-called indicators of

factors and processes as "indexes." However, two cogent reasons have caused the word indicator to be retained in the general as well as the special sense. The first of these is the impossibility of drawing a line between actual practices, as in agriculture, and the combination of human practice and natural process in forestry and grazing. The second is that the value of an indicator for practice rests upon the factor or process which it denotes. Furthermore, the term indicator has become so generally understood that it would be unfortunate to restrict its meaning, though it has been found convenient to employ "index" as a partial synonym.

Kinds.—The basic practices concerned in a system of indicators are agriculture, grazing, and forestry. The primary consideration, however, is which of these is possible or most desirable in a particular area or region. Since successful agriculture brings the largest returns per unit area, the first question is whether the land is agricultural. If not, the next question deals with its value for forestry or grazing, or for a combination of the two. The methods employed in reaching a decision as to the most desirable of the three practices constitute land classification, which in a new region at least is to be regarded as a practice prerequisite to the others. It is preeminently dependent upon plant indicators, as is shown by the first serious endeavor to classify the lands of the western United States upon anything approaching a scientific basis (Shantz and Aldous, 1917). It is obvious that similar methods, refined by quantitative methods and increasing experience, must sooner or later be used in all the new regions of the world where maximum economic returns are desired.

In addition to distinguishing areas as primarily agricultural, grazing, or forest land, practice indicators serve also to indicate particular types of agriculture, grazing, or forestry, as well as to suggest the crop of the greatest promise. Thus, in the case of agriculture, indicators may be used to denote the greater feasibility of humid, dry, or irrigation farming, or the importance of combining grazing with dry-farming. Where grazing is concerned, the type of vegetation not only determines whether cattle, sheep, or goats are preferable, or a combination of two or three possible, but it also indicates whether the introduction of other dominants is possible or desirable. In similar fashion, indicators may be employed to determine the possibility of afforestation or reforestation, as well as the most promising dominants for any particular region. Finally, practice indicators have more or less value for reclamation projects and other engineering operations, especially road-building, and they are of the first importance for indicating the course and intensity of climatic cycles and the modifications of current practice which they demand.

Because of their direct economic importance, a chapter is devoted to the indicators of each of the great basic practices, agriculture, grazing, and forestry, respectively. Land classification is considered in the following chapter in connection with agriculture, and the relation of climatic cycles to optimum production is discussed in connection with each type of practice.

PALEIC INDICATORS.

Paleo-ecology.—The significance of paleic indicators rests upon the conviction that ecologic processes were essentially the same during the geological past as they are to-day (Clements, 1916: 279; 1918: 369). It is assumed

that the vegetation of the globe was differentiated into climax formations corresponding to the primary climates. Such formations possessed a development and structure strictly comparable with that of present-day climaxes. They were divisible into associations, consociations, and societies, and they exhibited primary and secondary seres wherever bare areas occurred. The control of the direct factors, water, light, temperature, etc., must have been just as to-day, and this is equally true of their modification by physiographic processes and climatic changes, as well as by the competition and reaction of plant communities. Then, as now, the latter furnished food and shelter to the land animals, and these modified plant and community as a result of various kinds of disturbance. The conception of the biome, or biotic social unit, seems even clearer for past periods than for the present, owing to the lack of confusing detail, especially in the remoter eras. Finally, there is positive evidence of the minor climatic cycles, such as the 11-year sun-spot cycle, in the rings of fossil trees, and of greater cycles in the coseres of peat-bogs. Paleo-ecology is characterized, moreover, by great changes of flora and vegetation such as are unknown for ecology to-day. These are expressed in great successions, such as the clisere and eosere, which correspond with the grand deformational cycles.

Nature of paleic indicators.—While all the types of indicators now recognized must have existed in the past, especially if the Recent period is included, paleic indicators show one essential difference. This lies in the fact that communities were but rarely fossilized, and that the community itself must be inferred often from the merest fragments of its total population. Fortunately, the conception of the community as a complex organism with characteristic parts and processes furnishes an adequate method of interpretation. The great majority of species not only play a definite rôle in the climax or in its development as a dominant, subdominant, or concomitant, but each species also bears distinct relations to other species. When its rôle is interpreted in the light of its vegetation-form and habitat-form, it can be placed in the vegetation with something of the certainty possible in existing communities. As a consequence, the indicator values which have been taken for granted in all the preceding discussion, namely, the indication of other species, or even a whole community or sere by a single dominant or subdominant, play a paramount part in paleo-ecology. The smallest fragment of a fossil may thus become an indicator of the greatest significance, providing only that its generic identification be certain. In the case of plants at least, even this is not absolutely necessary if the vegetation-form or habitat-form be sufficiently distinctive to determine its habitat, and consequent position in climax or sere.

The methods of interpretation employed in paleo-ecology have been discussed in "Plant Succession" (p. 280), and summarized in a later paper (1918: 371). Because of its importance for the understanding of paleic indicators, this summary is quoted in full:

"The methods by which the ecological results of to-day can be carried back into the past have been briefly discussed in 'Plant Succession' and it will suffice to pass them in review here. For the most part these are methods with which the paleontologist is already familiar, since they have to do primarily with the translation of facts from the present to the past. The foremost is the

method of causal sequence, already mentioned, with its basic relation of habitat, plant, and animal. This is well illustrated by the occurrence of *Stipa* in the Miocene of Florissant, which indicates not merely the existence of prairie, but also, of course, a grassland climate and a grazing population. A similar but even more fundamental sequence begins with deformation and passes through gradation, climate, and vegetation to exhibit its final effects in the fauna. The *method of phylogeny* which has been the most serviceable of taxonomic tools is likewise of great value in the reconstruction of the life-forms and communities of the past. It shares with the method of succession the credit of permitting us to give more and more detail to the bold outlines of past vegetations and vegetation movements. The *method of succession* is based on the great strides made by the developmental study of vegetation during the last twenty years. When successional studies become the rule in zoo-ecology as well, there will seem to be no limit to the increasing perfection of detail in picturing the rise and fall of past populations and communities. In the case of vegetation, this method has recently gone so far as to bring conviction that all the essential features of successional processes and climax communities as seen to-day already existed in the past.

"As indispensable corollaries of the methods of phylogeny and succession are inferences from distribution in space and in time, and from association. The former enables us to close many a gap in the fossil record and to fill in the areas outlined by the known distribution of dominants. Inference from association, for example, aided by phylogeny, makes it all but certain that swamps of reed-grass, bulrushes, and cattails existed as far back as the Cretaceous, though *Phragmites* is the only one of the three dominants recorded for that period. The most recent is the *method of cycles*, which gives promise of becoming one of the most important. It is perhaps too soon to insist that cyclic processes are universal in time and in space; but the great mass of evidence from geology and climatology is matched by an increasing body of facts from biological succession."

Kinds.—The indicator values of a fossil plant or animal clearly depend upon the accuracy of its identification and stratigraphic position. With reference to the former, its generic position, together with the vegetation-form and habitat-form, is of paramount importance, partly because specific determinations are often very uncertain among plants at least, and partly because the majority of genera are uniform as to the ecological type of their constituent species. While definite stratigraphic allocation is necessary for finer analysis, the assignment of a plant to a particular era or period has much value, owing to the fact that many dominant genera persist throughout most or all of an era. The indicator value also depends greatly upon whether the plants were fossilized in position and hence in their community relations, or whether they have been scattered and carried to points more or less remote from their home. The distinction between the corresponding deposits, termed stases and strates, is discussed at some length in "Plant Succession" (291). Here it will suffice to point out that the water stase as exemplified in peat-bogs has nearly the complete indicator values of an existing sere, while those of the much more universal strate are usually incomplete and subject to interpretation.

It is evident that fossil plants, and animals also to a lesser degree, may serve as indicators of factors, processes or practices, in essentially the same way that existing species do. Practice indicators are naturally connected

with the presence of man, and hence are restricted to the Pleistocene and Recent periods. Grazing must have been the earliest of these, perhaps reaching back into the late Pleistocene, but agriculture was relatively well-advanced by the time of the Lake-dwellers, and construction, as well as a crude sort of forest utilization, was at least begun. Moreover, it must be recognized that, while grazing took on some new features as herds came under the control of man, it must have existed as a natural process throughout the Tertiary at least. In the case of fire, this agency must have begun its modifying influence upon vegetation as early as the Paleozoic, but its effect must have greatly increased with the differentiation of deciduous forest and grassland in early Tertiary times. It could hardly have become a universal process until the pastoral phase became general, and its greatest extension has doubtless taken place during the last 1,000 years. The primary processes involved in physiographic and climatic changes must have had much the same indicators as to-day, allowing for the differences in flora during the various eras. While such changes seem much greater and more frequent during the geological past than to-day, this is almost certainly the result of a short perspective. With respect to factor indicators, the plant genera concerned during the Cenozoic era were largely those which characterize marked differences in water, light, and temperature to-day, and this was particularly true after the Miocene. During the earlier eras, the genera were mostly different, but the vegetation- and habitat-forms the same.

The fragmentary nature of the fossil record makes it necessary to emphasize certain existing indicator relations, as well as to employ some not needed in actual vegetation. These are derived from the methods of interpretation already discussed. The use of indicators based upon the successional sequence is much the same, except that a single dominant or stage must often serve to denote the presence of the entire sere. Even this is not so different from conditions to-day, since there are many swamps in arid regions especially in which the reed-swamp associes is represented by *Scirpus* or *Typha* alone. The method of causal sequence furnishes many of the most striking and significant of paleic indicators. Habitat, plant, and animal are linked together in a fundamental cause-and-effect relation, in which each one serves as an indicator of the other. The importance of the plant in this relation has been emphasized elsewhere. It may be said to have a double indicator value, since it indicates the habitat directly by its response, and the animal directly by virtue of the control exerted through food and shelter. Thus, while there are numerous examples of definite relations between habitat and land animals, most of these take the plant community for granted. The indicators of cycles comprise both those derived from succession and from causal sequence. In fact, they are the indicators of the grand successions recorded in the clisere and eosere, and consist chiefly of shifting formations and floras. Fossil genera and families often possess great indicator values which arise from their phyletic relationships. While phylogeny must long remain a field for varied opinions, certain great lines of relationship receive increasing recognition, and can be employed with corresponding certainty. Thus, while *Juncus* is not recorded until the Eocene, the presence of both *Carex* and *Phragmites* in the Cretaceous makes it all but certain that the more primitive *Juncus* was already in existence. In connection with phylogeny and

succession, plants may indicate distribution in space and in time as well as the presence of associated dominants (Plant Succession, 352).

Since the field of indicators has been developed wholly with reference to plants and with particular application to agriculture, the importance of reciprocal indicators has not been recognized. However, in paleo-ecology where the body of definite facts is relatively small, it is of the greatest aid to secure all possible indications from every fact, and to check these by the indications of related facts. Fossil plants and animals constitute the best of reciprocal indicators, but topography and climate are often of great service also. When all four can be employed as indicators in a particular period or region, it is possible to reconstruct the biome in much detail and with the greatest possible certainty. For example, the geologic evidences of arid climates at different periods must be regarded as more or less tentative until confirmed by plant or animal indicators of aridity. When both occur, as in the Miocene, the chain of evidence is complete. It then becomes possible with the aid of the indicator relations discussed here to present a fairly detailed and complete picture of the structure and development of the biotic climaxes of the past. The general features of this have already been done for animals by Osborn (1910), and much progress has been made in doing this for the associated plants and animals of the Bad Land horizons of the West.

Paleic indicators of climates and cycles.—The evidences of past climates and climatic changes have been summarized from the geologic, botanic, and zooic aspects (Plant Succession, 313). Since plants are the most immediately responsive to climatic influences and constitute the best indicators, they are chiefly considered here. The grand climates of geologic time are indicated by corresponding great floras and faunas, which have served as the basis for the division into eras. During each of the latter, climatic differentiation in both space and in time has been faithfully reflected in the vegetation, and the combined effect of climate and vegetation in the fauna. It seems highly probable that a considerable differentiation of climates and climaxes took place during the Paleophytic era, and that this was increased during the Mesophytic era to become the most outstanding feature of the biosphere during the Cenophytic. Thus, while each era is indicated by a particular climax flora, it also exhibits climax formations as indicators of more or less distinct climates, just as is the case to-day. While the grand deformation cycles which produced the eras were marked by a changed flora and fauna, the major deformation cycles and grand sun-spot cycles are thought to correspond with shiftings of climate and vegetation, such as are indicated for the Pleistocene. These have to do with climaxes as indicators, and it seems a fair assumption that the series of climaxes found in the Pleistocene shiftings likewise occurred in some degree in the earlier cliseres of the Mesophytic and Paleophytic eras. The constitution of the climaxes during the various eras and their relation to climatic cycles is discussed in some detail in "Plant Succession" (356, 406, 419) and need not be repeated here.

Paleic indicators of succession.—Apart from the great successional movements involved in the change of floras and the shifting of climaxes, there must have been innumerable examples of seres and coseres in every era. Primary areas of erosion and deposition were probably more abundant than to-day, and primary succession must have been the rule, though secondary seres were

not unknown. Coseres resulting in the formation of coal or peat have occurred repeatedly from the Paleophytic to modern times, while in periods of great volcanic activity, such as the Miocene, they were produced by deposits of volcanic dust. While each era possessed its particular flora, all the life-forms were represented. Thus, while the genera typical of the various seral stages during the Paleophytic and Mesophytic are practically all different from those of the Cenophytic and to-day, the vegetation-forms and habitat-forms are the same or nearly so. With reference to the genera which constituted the seral dominants and hence served as indicators of habitats and of succession, the life-forms have been discussed in "Plant Succession" (pp. 354, 405, 420). Throughout the major portion of the Cenophytic, the seral genera as well as the life-forms were essentially the same as those of to-day, and their indicator value is readily inferred from existing conditions.

Plant indicators of animals.—The general indicator relations of fossil plants and animals have long been recognized and utilized by paleontologists, but chiefly on the animal side. The correlation between the appearance of a dominant angiospermous flora and the evolution of mammals is the most outstanding example of this, but the rise of the cursorial ungulates in response to an expanding grassland climax is hardly less striking. Such correlations must be superlatively general before the Cenophytic, though the existing relations between seral and climax communities and the great groups of animals must have had analogies at least during the Mesophytic era. Since the larger animals were all totally different, and the dominant genera of plants practically all different likewise, the use of plant and animal indicators as a basic method in paleo-ecology must be confined chiefly to the Cenophytic era for the present. Here, however, it seems to offer great possibilities, some of which must wait upon the further study of communities as biotic units with development and structure. The indicator value of plants in this connection is limited only by our knowledge of existing correlations with animals. This is due to the fact that a large number of modern genera of plants have existed since the Cretaceous. The evolution of animals has been much more rapid, and the number of existing genera of mammals, for example, which reach back to the Eocene is very small. However, among the rodents and ungulates, where plant correlations are most important, nearly half the families contain both modern and fossil genera. With respect to the birds and insects, our knowledge is much less complete, but it appears highly probable that many existing families and orders had arisen at least by the Tertiary. As a consequence, it becomes possible to scan the rapidly growing list of plant indicators, and to extend their correlations as far into the past as the recorded existence of the genera or related genera permits.

Animal indicators of plants.—The reciprocal relation of plants and animals as indicators, whether as communities or species, greatly extends the use of indicators in geological times. In many horizons, animals have been preserved to a much larger degree than plants, while in some, plant remains are entirely lacking. Fossil animals are especially significant in the reconstruction of upland life, since the cursorial forms of the uplands were preserved in fairly large number, while the record of the associated plants is exceedingly fragmentary. Moreover, animals may serve to indicate the presence of plants in regions or in periods where they are not yet actually found. Outside

of the insects, there are few extinct animals in which there is an indicator correlation with a single species of plant. On the other hand, the correlation of herbivores with plant communities, both climax and seral, is practically universal, and they serve to indicate with a high degree of probability the development and extension of sedgeland and grassland from the Cretaceous to the Pliocene. The general correlation of browsing ungulates with forest and scrub, of the earlier types of grazing animals with sedgeland and meadow, and of the highly specialized upland types with the climax grassland of xerophytic grasses (Osborn, 1910: 9, 237) is fundamental, and has been used to furnish the basis for the treatment of the development and structure of the biotic communities in the Bad Lands of the West.

XIV. AGRICULTURAL INDICATORS.

General relations.—As the basic economic practice of plant and animal production, agriculture furnishes the standard for measuring the possibilities of soils, climates, and regions. There are many reasons for this, chief among them the fact that it gives relatively large and immediate returns upon a small capital. In addition, its operations are within the scope of the individual or family, and farming has inevitably become the traditional basis of the American homestead. The latter has played such a wonderful rôle in the development of the West that it has come to be regarded as a fetich, able to reclaim the most arid desert or to enrich the most sterile soil. During the last two decades the large majority of the homesteads filed upon have proved failures and the percentage of failures will steadily increase as still less promising regions are entered, unless the method of settlement is radically changed. The time when individual initiative would suffice to convert a tract of virgin land into a prosperous farm has gone. While millions of acres of public lands still remain for settlement, these are of such a nature that land classification, reclamation, demonstration, and cooperation are indispensable to their conversion into successful farms and ranches.

LAND CLASSIFICATION.

Nature.—The classification of land is an endeavor to forecast the type of utilization that will yield adequate or maximum returns. Properly, it should determine the optimum use as accurately as possible, and should insure the conditions under which development and utilization take place. In actual practice, classification has been conspicuously absent as a preliminary to the settlement of the arid regions of the West. Hurried and incomplete classifications have been made for special purposes, but these have covered only certain portions of the vast public domain and have usually suffered from inadequate and hasty methods. Perhaps their greatest fault has been that they were made with a particular end in view, and the primary object was to include or exclude as much land as possible without reference to its optimum utilization. In this respect the recent classification under the Ferris Act has been an improvement, but it has been handicapped by legislative restrictions and by the lack of an adequately trained field personnel. It has been especially unfortunate that only those lands were examined which had been filed upon, with the result that the examiner's judgment or decision was often influenced by local pressure. To the one who is interested solely in seeing the public domain developed in such a way as to secure the best economic and social conditions, it is incomprehensible that the prerequisite of an accurate and unbiased classification of the land should have been so long ignored.

Such a land classification would necessarily take account of the enormous amount of scientific reconnaissance and investigation done in the West, during the last thirty years especially. It would rest upon a rapidly increasing fund of practical experience and experimental study of crops and methods, and upon the paramount importance of drought periods and their recurrence in climatic cycles. In method, it would be complete, detailed, accurate, and

unprejudiced, availing itself of all sources of information, but based primarily upon the relation of indicator vegetation to existing practice. The most difficult problem would be that of a large, adequately trained, and high-minded field force, but the rapid development of the Forest Service has shown how this can be accomplished.

Relation to practices.—While land classification is based primarily upon the division into agriculture, grazing, and forestry, other considerations must also be taken into account. At the outset, it is particularly important that the future as well as the immediate present be considered. Many areas which are non-agricultural at present can be made available for crop production by the development of a supply of irrigation water or by the draining of the soil to remove the excess of alkali. On the other hand, the extension of agriculture into mountain regions on a considerable scale would threaten the water-supply of existing irrigation projects. The maintenance of forests on a scientific basis is more than a matter of the present demand for lumber and fuel. It has a definite and often a decisive bearing upon the agricultural possibilities of the land in the adjacent valleys and plains. Moreover, questions of reforestation and afforestation enter in relation to agriculture and grazing, and perhaps to climate also. While the use of land primarily for agriculture excludes forestry or grazing on any considerable scale, this is not true of the latter. Under proper safeguards, forestry and grazing can be combined in practically all forest and woodland areas, as is the case on the national forests. It is not improbable that the extensive sandhill areas of the Great Plains region will some day be covered with forests of pine without seriously reducing the amount of grazing, and in some cases with an actual increase in the permanent carrying capacity.

The greater returns from agricultural land and the consequent possibility of supporting a larger population will always constitute a temptation to classify too much land as agricultural. If classification could be carried out only during drought periods, this tendency would be corrected. On the other hand, it would be emphasized during wet years, such as 1915, when many regions received 50 to 100 per cent more than their normal rainfall. As a consequence, the classification of land as agricultural must be made with a definite knowledge of the existing conditions of rainfall and temperature and their relation to the usual variations of the climatic cycle. Moreover, it must be recognized that it is much less serious to classify a potential agricultural area as grazing or forest land than to classify the latter as agricultural. The former merely involves an insignificant economic waste until the real possibilities of the land become recognized, while the latter often results in recurring tragedies due to the attempt to make a livelihood where it is impossible. Hence, it should become a cardinal principle of land classification to rate as grazing or forest land all areas in which it is impossible to produce an average crop three years out of four. This would insure an adequate and permanent development of agriculture wherever possible and would warrant the introduction of scientific and economic systems of grazing, which would change it from a game of chance into an industry.

Proposed bases of classification.—While soil and climate have been employed in connection with various desultory atempts at classification, the

only proposals which need to be considered here are those which deal with indicator vegetation. The latter necessarily takes account of both soil and climate and furnishes the only basis for an adequate system. The first serious proposals of such a system were made by Hilgard, as already shown in the first chapter. As a student of soils, he was concerned primarily with the indicators of soils (1906: 487), and especially those which were regarded as significant of lime or alkali. He paid almost no attention to indicators of climate, and was concerned only with those which denoted agricultural land. Because of his primary interest in the distribution of animals, Merriam (1898) emphasized the importance of climate in agriculture, and ignored that of soil. His central idea was to enable the farmer "to tell in advance whether the climatic conditions on his own farm are fit or unfit for the particular crop he has in view, and what crops he can raise with reasonable certainty." Hence, he was concerned with a use survey rather than with land classification, though his "life zones and crop zones" possess certain values in connection with the latter.

Clements (1910: 52) pointed out the difference between a classification survey and a use survey of occupied lands, and emphasized the necessity of employing soil and climate, native vegetation, and practical experience to constitute a complete system for classifying the lands of a region as agricultural, grazing, and forest. Several unoccupied townships of northern Minnesota were classified on this basis and several farming townships of the southern half were mapped in accordance with a use survey. The investigations of Shantz (1911) in eastern Colorado dealt chiefly with the indicator value of the different associations with reference to crop production and furnished a new basis for the classification of agricultural land with respect to probable yield. A similarly detailed and accurate study of the saline vegetation of Tooele Valley was made by Kearney and his associates (1914), in which the primary object was to provide a definite method of distinguishing agricultural from non-agricultural lands and of determining the relative values of the former.

The rapid establishment of national forests from 1902 to 1908 necessitated the use of a ready method of distinguishing between forest and agricultural land. The indicator method had not yet been definitized to a point where it was available, and studies of soil and climate were barely begun. In spite of this, forest and woodland constitute such obvious indicators that their use afforded fairly satisfactory results, particularly when water regulation was taken into account. The limits of the forests thus drawn necessarily included some agricultural land as well as great areas of grazing land. Much of the former has later been eliminated by reclassification, while the latter has been classified into various types (Jardine, 1911, 1913). Within the forests proper, the problem of classification has naturally revolved about the question of forest types. This has given rise to an extensive literature (Graves, 1899; Zon, 1906; Clements, 1909; cf. Proc. Soc. Am. For., 1913: 73) and is discussed in some detail in Chapter XVI. Pearson (1913: 79; 1919) has emphasized the importance of ascertaining the agricultural possibilities of forested land in order to determine with certainty whether it should be classified as one or the other. He proposes a definite program of investigation to make the principles and methods of land classification more accurate. This is based

upon actual tests of agricultural possibilities, the study of physical factors, and the correlation of crop production and plant associations, the last being regarded as the most important feature of the whole plan.

The most extensive and adequate application of the proper principles of land classification to the lands of the West has been made in connection with the stock-raising homestead act of 1916. This is based primarily upon the indicator method, and the details have been outlined by Shantz and Aldous (1917). While the primary object is to classify the areas filed upon for grazing homesteads, it has proved necessary to deal with the classification of agricultural and forest lands as well. In this connection the latter are relatively unimportant, but the recognition of lands for dry-farming is an essential part of the plan. This arises from the fortunate provision that a grazing homestead must contain areas on which it is possible to produce crops of forage. As already indicated, the only drawbacks to the method arise from an untrained personnel and the lack of sufficient time for adequate survey. The correlation of the indicator types upon the basis of structure and development would have revealed additional values, but the plan marks a great advance in land classification and it is unfortunate that its application is restricted to lands filed upon under the act.

The indicator method of land classification.—As the above discussion makes clear, practically all the effective proposals for classifying land into the three main types, or for subdividing these upon the basis of crops or values, rest upon the fundamental significance of indicator plants and communities. The systems proposed by Clements, Pearson, and Shantz and Aldous, though arrived at from three different angles, are practically identical so far as essentials are concerned. They recognize the importance of actual practice and experiment as well as of quantitative studies of soil and climate in definitizing the correlations of the indicator communities. The latter, however, constitute the indispensable tool of the land classifier, since its use is as ready as it is extensive and is limited only by its accuracy and sharpness. In the hands of a well-trained field force, it would permit the proper classification of all the unoccupied lands of the West within a period of five years. The essentials of such a classification are further discussed in a later section.

Use of climax indicators.—It is clear that the climaxes themselves furnish direct indications of great value for land classification. Thus, grassland, chaparral, and scrub are obviously indicators of grazing land, while forest and woodland are indicators of forest land. However, these comprise all the types, and a different method is necessary for the determination of agricultural land. This may be furnished by actual test, by the measurement of factors, or by the use of indicator correlations already established in other regions. As a matter of fact, some kind of farming test can be found almost anywhere in the West, in the driest deserts as well as at almost any altitude. The studies of the last decade have made the application of indicator correlations almost universal, and the measurement of soil and climatic factors has at least been begun in practically every climax. As a consequence, it becomes a relatively simple matter to use climax communities to indicate those grazing and forest lands which are also agricultural, in that they yield a larger return from crop production than from grazing or forestry.

In the West, the climax which serves as the best indicator of crop production is naturally grassland. As the most extensive of all the formations concerned, its various associations serve also to indicate all the types of farming from humid and semi-arid on the east to dry-farming and irrigation farming in the west. While the alpine meadow climax has many points of resemblance to the grassland, it is a clear-cut indicator of grazing land, since neither trees nor crops can thrive in it. The various scrub climaxes, sagebrush, desert scrub, and chaparral, as well as tree and scrub savannah, are primarily indicators of grazing land, unless irrigation is resorted to. Dry-farming is possible in certain areas in them, but these are usually in the transition to other formations or in the seral habitats. A notable exception occurs in the Coastal chaparral, in which the winter rainfall makes certain crops possible by evasion of the drought period of summer. The woodland climax is primarily an indicator of combined forest and grazing land. It has some agricultural possibilities, but these are rarely to be realized except under irrigation. Of the three forest climaxes, the Coast forest is a distinct indicator of crop production and the subalpine forest is just as distinctly an indicator of non-agricultural land. The montane forest in general is like the subalpine in indicating forest-grazing land, but this depends upon the consociation and topography. The yellow pine consociation often indicates agricultural land, but the indication of the community must be checked by the nature of the topography and soil.

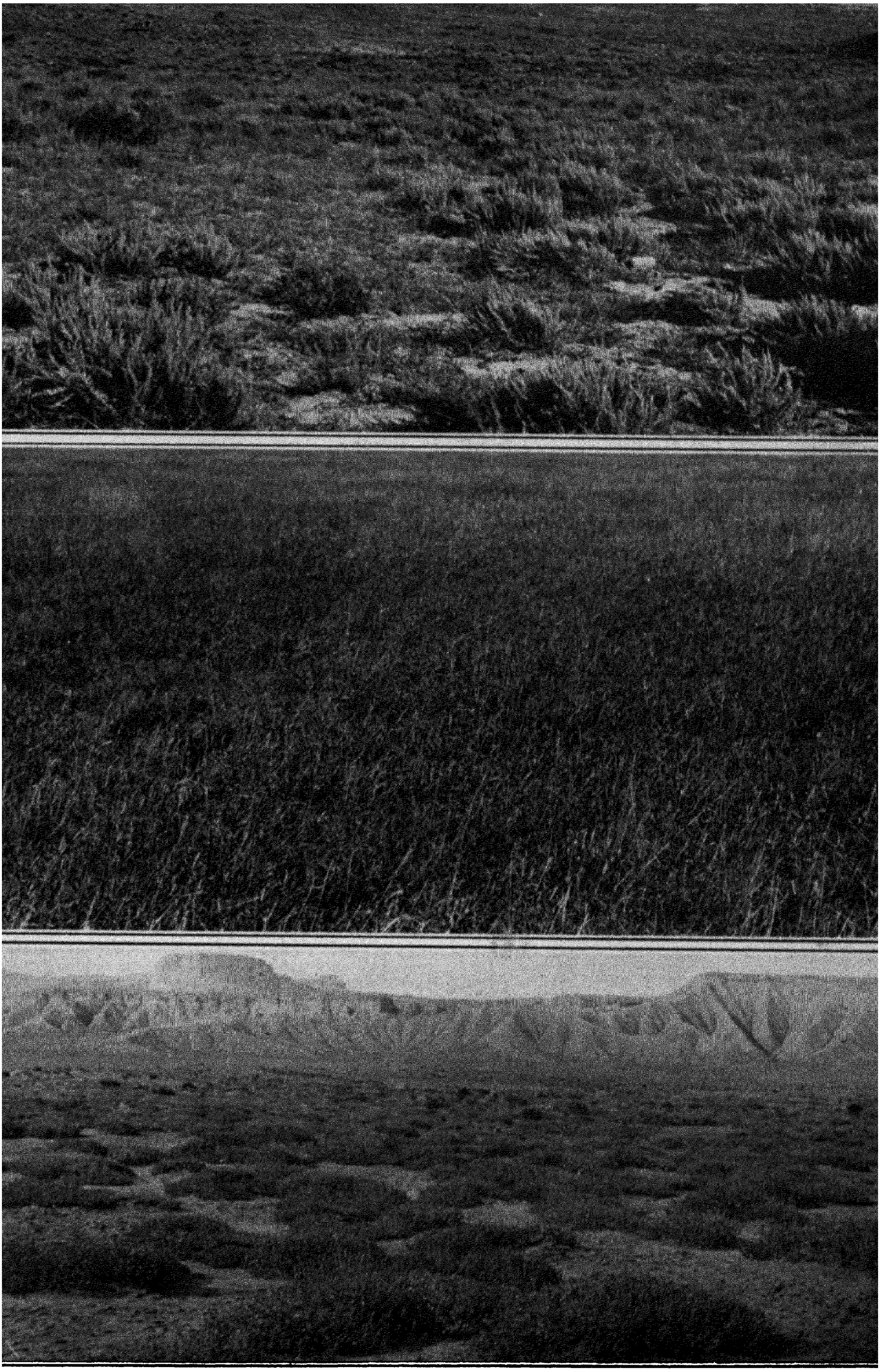
In the case of all climaxes, the relations of formation, association, consociation, and society to each other lie at the basis of the indicator correlations of the various communities. The indicator value of an association must be understood with reference to its formation, and that of the consociation with reference to its association. In general, these will be consistent with each other, and hence they serve to denote smaller and smaller areas, and particular crops and methods rather than types of practice. This is especially true of the many local groupings of dominants and subdominants. The societies formed by the latter are particularly sensitive indicators of local variations in climax conditions (Shantz, 1911).

Soil indicators.—The significance of soil indicators is local, as well as subordinate to that of climax or climatic indicators. The soil is especially important in the actual practice of land classification, since it is more tangible than climate and is subject to much greater local variations. Consequently, in any particular region climax indicators should be employed for general climatic values, while soil indicators should be used for the special values which will determine the proper classification of a particular area. In view of the paramount importance of water-content in arid and semi-arid regions, the general correspondence between rainfall and water-content from east to west becomes especially helpful. While texture and topography will cause soils to vary much locally in their water-content, the water-content of tillable soils decreases more or less steadily to the westward or southwestward. This relation of climate and soil is readily seen in the soil regions of the West as recognized by the Bureau of Soils, namely, Great Plains, Rocky Mountain, Southwest Arid, Great Basin, Northwest Intermountain, and Pacific Coast. As would be expected, these regions also show more or less correlation with the climax formations.

The loess and glacial soils of the prairies are so completely cultivated that they hardly need consideration as to their indicators. The luxuriance of the three prairie associations and the large number of societies, especially of legumes, denote an agricultural region of the first importance. To the westward, the most extensive and important soils are gumbo or hard-land, saline soils, and sandy soils, usually of the sandhill or dune type. Where it is derived from the weathering of shales, as is frequently the case, the soil is usually both gumbo and saline. As Shantz (1911) has shown, hard-land is primarily agricultural in the Great Plains, though its high echard is a serious disadvantage during drought periods. Soils recently derived from shales, such as the Pierre and the Graneros, however, bear a vegetation which suggests that their greatest value is for grazing. The work of Hilgard (1906) and of Kearney and his associates (1914) has shown that, in the Great Basin and similar saline regions, sagebrush is the one reliable indicator of agricultural land. While crops may be produced on land covered with *Atriplex confertifolia* or *Kochia,* it is only during years of exceptionally favorable rainfall, which are too rare for successful farming. Hence, practically all saline communities are indicators of grazing land, though such land may be converted to agricultural use when the removal of alkali is economically feasible.

The numerous sandhill and dune areas of the West bear distinctive indicators which denote the varying degrees of fixation of the sand. Typically, they are grazing areas, though they are usually interrupted or surrounded by more stable areas, such as the wet valleys of the sandhills of central Nebraska or the wire-grass lands of eastern Colorado, in which farming is possible. Even for grazing, their value is much less than it should be, and in addition there is a rapid deterioration of the cover where overgrazing is practiced. There is no question that the carrying capacity could be greatly increased and the tendency to "blow" correspondingly decreased by protection and seeding or planting. The Bad Lands, which occur throughout the West, but especially in the Rocky Mountain region, likewise offer attractive districts for reclamation. Although the soil is a hard clay instead of blow-sand and the erosion is due to water in place of wind, sandhills and bad lands have much in common. The destruction due to erosion is often rapid and complete, as well as recurrent. They occur almost wholly in grazing communities, and the study of succession in both has reached a point where it is possible to make use of it as the chief method of reclamation, as is shown in Chapter XV. The extremely dissected topography of bad lands practically excludes agriculture, and in general the communities of rugged and rocky areas indicate their classification as grazing lands, even when climatic conditions might permit agriculture. In the case of swamp and bog communities, the direct indication is for grazing, but since they need drainage in order to be put into adequate commission, their classification should take this into account. When they are not too high or too far north, the drained areas will permit farming, but when they occur in the montane zone, or above, their chief value is for grazing (plate 30).

Shantz's results.—Shantz's studies of indicators in eastern Colorado are still the most complete and detailed account of the correlation of indicator communities and soil. His conclusions apply with slight modification to the entire short-grass association, and they also have much value for mixed prairies:



A. *Artemisia filifolia* indicating sandy soil, Canadian River, Texas.
B. *Bouteloua* and *Bulbilis* on hard-land, Goodwell, Oklahoma.
C. *Atriplex nuttallii* indicating non-agricultural saline land, Thompson, Utah.

"The chief plant associations of eastern Colorado which indicate land of agricultural value are the grama-buffalo-grass association and the wire-grass association (both of which belong to the short-grass formation) and the bunch-grass association and the sand-hills mixed association (both of which belong to the prairie-grass formation).

"The chief vegetation types of eastern Colorado which indicate nonagricultural land are the lichen formation, the *Gutierrezia-Artemisia* association of the short-grass formation, and the blow-out association of the prairie-grass formation.

"Of the associations indicating land of agricultural value in eastern Colorado, the grama-buffalo-grass association is most extensive, occupying the greater part of the hard land. The bunch-grass and the sand-hills mixed associations occur only in the sand-hill regions, while the wire-grass association occurs on land of intermediate character.

"In eastern Colorado the rainfall records show that the average monthly rainfall is greatest during the period April to August. The increased heat in July and August makes it almost certain that drought will occur in these months. September and the later fall months have normally very little rainfall, and fall-sown grain often fails to germinate unless planted on land in which water from rains earlier in the season has been conserved by summer tillage.

"Measurements show that from grama-buffalo-grass land a great amount of water runs off and does not enter the soil.

"Soil-moisture determinations in this type of land show that even during periods of more than normal rainfall available soil moisture is limited to a few inches of the surface soil.

"On this account the vegetation is composed largely of short grasses which have a great number of roots limited to the surface foot or two of the soil.

"Moisture, even in the surface few inches of the soil, is often lacking except during a few weeks in spring and early summer. The short grasses have a comparatively short growing season.

"Deep-rooted species are shut out by the lack of soil moisture in the deeper layers of the soil and later-season plants are excluded because available moisture is usually lacking, even in the surface layers, during late summer and autumn.

"An open cover of the short grasses indicates conditions less favorable for crop production than a close cover.

"The presence of deeper-rooted plants mingled with the short-grass vegetation indicates better conditions for crop production than those found where the cover is purely of the short grasses.

"The occurrence among the short grasses of plants characteristic of the associations which indicate land without agricultural value suggests a less favorable condition for crop production than where short grasses only are found.

"The presence of the wire-grass association indicates that there is a considerable amount of water in the deeper layers of the soil, owing to the lesser run-off and to the fact that the lighter soil permits deeper penetration.

"Conditions indicated by the wire-grass association are favorable for both shallow-rooted and deep-rooted plants and for a considerably longer period of growth than those indicated by the grama-buffalo-grass association.

"The bunch-grass association indicates a soil that is moist to a considerable depth. Here conditions are more favorable for deep-rooted and late-season plants than in land characterized by either the short-grass or the wire-grass vegetation.

"The sand-hills mixed association indicates conditions very similar to those of the bunch-grass association, but rather less favorable, as shown by the smaller amount of plant growth.

"The short-grass vegetation represents the final stage in a succession which may begin with the lichen formation and pass through the *Gutierrezia-Artemisia* association. Or the succession may begin with the blow-out association and pass through the sand-hills mixed and the bunch-grass associations and (by the aid of fires and grazing) through the wire-grass association to a pure short-grass vegetation.

"When short-grass land is left without cultivation after breaking it will be revegetated by either the wire-grass or the *Gutierrezia-Artemisia* association, depending upon the physical conditions.

"The vegetation which establishes itself after wire-grass is turned under is that which is naturally characteristic of a lighter soil.

"When the native sod of the bunch-grass or the sand-hills mixed associations is broken, a blow-out may result. Usually, however, the original vegetation is soon reestablished.

"When the vegetation of any of the plant associations is destroyed by breaking and the land is then abandoned the land will be reoccupied (after a weed stage) by vegetation that is characteristic both of a lighter type of soil and of an earlier stage in the natural succession. These successions are the result of changes in the physical conditions brought about largely as a result of the destruction and reestablishment of the plant cover itself.

"The taller, deeper-rooted plants are easily shut out by the shallow-rooted short grasses when the water that falls as rain is not sufficient to penetrate beyond the layer of soil occupied by the roots of the short grasses before it can be absorbed by them.

"Where water can readily penetrate below the depth ordinarily reached by the roots of the short grasses the conditions are favorable to the growth of deeper-rooted and taller species, which shut out the short grasses by overshading them. This increased penetration of water may be due either to greater rainfall or to lighter soil texture.

"When well supplied with water short-grass land is the most productive under cultivation of any in eastern Colorado. During drought, however, crops suffer on this land sooner than on any other type.

"During exceptionally dry years bunch-grass land produces the best crops of any in eastern Colorado, but during wet years its production is surpassed by that of all others except the land characterized by the sand-hills mixed association. The soil under both of these types of vegetation is likely to blow badly.

"Wire-grass land represents a safe intermediate condition where in years of ample rainfall crop production compares not unfavorably with that on short-grass land and where, even during dry years, a fair crop can often be produced.

"One of the chief reasons for the superiority of light land over heavy land in eastern Colorado is that crop growth is rapid on the latter and that the total available supply of soil water lies near the plant roots, the crops, therefore, being in somewhat the same condition as potted plants. These conditions favor a rapid exhaustion of soil moisture and, consequently, bring about sudden drought. On the lighter land water is distributed to greater depths, the plant growth is slower, and plants, by gradually increasing their root area, can resist much longer periods of drought.

"Investigations of soil conditions, as well as actual observations of crops in the field and studies of the native plant cover, show that as we pass from the prairie westward to the more arid portion of the Great Plains, the lighter

soils present relatively more favorable moisture conditions and, therefore, conditions more favorable to plant growth than do the heavier types of land."

A SYSTEM OF LAND CLASSIFICATION.

Bases.—As has been repeatedly emphasized, a system of land classification which is both practically and scientifically adequate must ignore no source of evidence. While indicator vegetation must be regarded as the chief tool, the latter is valueless unless it is correlated with practical experience and experiment on the one hand and with factor measurements on the other. Some indicator values can be disclosed by the use of a single one of these correlations, but all of them are necessary for complete certainty and accuracy. They not only serve to check each other, but also to reveal additional and final values. Furthermore, it must be recognized that all the climatic and hence many of the soil factors vary considerably and sometimes critically from year to year, and that this means a corresponding difference in crop production, and often in tillage methods. As a consequence, the annual variations in factors, indicators, and production must always be taken into account and related, as far as possible, to an average or norm. The normal rainfall or mean temperature is insufficient for this purpose, especially since it fails to disclose the number and occurrence of the critical dry years. For this purpose the use of climatic cycles is necessary, and in consequence they must be assigned an important part in the classification of lands in arid and semi-arid regions. The existence and effect of such cycles are established beyond a doubt, and the chief task at present is to learn how to make the fullest possible use of them. This naturally depends upon the certainty and accuracy with which the dry and wet phases of the cycle can be predicted (Clements, 1917:304, 1918:295). The nature and utilization of climatic cycles are discussed in the following section.

Classification and use.—The close relationship between classification and use surveys and the importance of developing the one into the other can hardly be emphasized too strongly. The vital connection between the two in the proper development of the possibilities of the land may be seen from the following (Clements, 1910:52):

"The first step in determining the final possibilities of plant production is to ascertain just what the conditions of soil and climate are from the standpoint of the plant. This must be determined separately for the two great groups of lands, those still unoccupied and those now in use. For the former, a knowledge of soil and climate, and of the plant's relation to them, is necessary to decide what primary crop, grain, forage, or forest, is best. For the farms of the State, the best use is a matter of knowing the soil and climatic differences of regions and fields, and of taking advantage of this in crop production. For the unoccupied lands of Minnesota, we need a classification survey to determine the best use of different areas; to prevent the waste of human effort and happiness involved in trying to secure from the land what it can not give, and yet to insure that the land will reach as quickly as possible its maximum permanent return. For occupied lands, the study and mapping of soil and climatic conditions would constitute a use survey of the greatest value in adjusting plant production to the conditions which control it.

"A use survey is the logical outcome of the classification of land. Its greatest importance is with agricultural lands, since grassland and forest

permit less specialization in crop production. The period of the one-crop farm seems nearly closed; that of the special-crop farm is barely begun in this country. As a method of conservation, diversified farming is a permanent step in advance. It is the foundation upon which a distinctively successful country life is possible. But intensive cultivation is the open secret of scientific farming, and it demands the closest possible harmony between the plant machine, the raw materials which it uses, and the conditions under which it works. This makes possible the successful specialization of a region in the crop best adapted to the soil or climate more or less peculiar to it. The task of a use survey in this connection is to determine the special advantage of soil or climate, and to suggest the particular kind of plant machine and the method of production adapted to it. The same careful method of survey, which makes possible the best use of the different agricultural lands of the State, is likewise of great value on the individual farm, whenever differences of soil or exposure exist. The general nature of the soil and climate of a farm must determine its special crop, and in a degree the secondary crops as well. But the complete success of the farm will rest upon a thorough knowledge of its differences of soil and climate, as well as upon a knowledge of the best varieties to grow or the best way to improve them."

Methods.—While it is undesirable to discuss in detail the actual methods of classification and use surveys, it must be pointed out that they depend in the first instance upon accuracy and thoroughness. This is exemplified in the work of the Botanical Survey of Minnesota (Plant Succession, 436), in which the natural and cultural vegetation was mapped for every "forty" of the townships concerned, and quadrats, instruments, and photographs were employed throughout. Similar though less detailed methods have been used in the grazing reconnaissance of all the national forests (Jardine, 1911) and in the classification of grazing homesteads under the Ferris Act (Shantz and Aldous, 1917). The essential features of these are touched upon in the discussion of the methods of range survey in Chapter XV.

A logical and desirable outcome of a classification survey is a valuation of the various parcels of land, with respect to both leasing and purchase. It has been a natural assumption that the nation could well afford to dispose of the public domain at merely nominal prices, and such a policy was warranted in the Middle West. In the arid regions, however, values vary so greatly that it constitutes a serious mistake. This is readily seen when it is recognized that the best grazing lands will support more than 100 cattle to the section, while the poorest will support scarcely one. This is particularly true in the case of leasing, where proper valuation based upon actual carrying capacity will determine whether lands are to constitute a public asset or to be the usufruct of politicians. While the nation or State can afford to be generous to bona fide settlers, it can treat them all alike in fact only by fitting prices to the production value of the land and by making the operations of the speculator difficult if not impossible. Moreover, it should insure the success of each settler by means of use or management surveys which will give him a detailed and adequate knowledge of his particular farm and of the crops and methods to be used upon it. Since such surveys are of the greatest importance in connection with the combined grazing and dry farming which it seems must become typical of the West, their further discussion is deferred to the next chapter.

CLIMATIC CYCLES.

Nature.—The general nature of climatic cycles as well as their universal occurrence and fundamental importance is summed up in the following statement (Plant Succession, 329):

"It is here assumed that all climatic changes recur in cycles of the most various intensity and duration. In fact, this seems to be established for historic times by Huntington and for geologic times by the studies of glacial periods which have made possible the table compiled by Schuchert. The cyclic nature of climatic changes has been strongly insisted upon by Huntington: 'The considerations which have just been set forth have led to a third hypothesis, that of pulsatory climatic changes. According to this, the earth's climate is not stable, nor does it change uniformly in one direction. It appears to fluctuate back and forth not only in the little waves that we see from year to year and decade to decade, but also in much larger ones, which take hundreds of years or even thousands. These in turn seem to merge into and be imposed upon the greater waves which form glacial stages, glacial epochs, and glacial periods.'

"Climatic changes, then, are assumed to be always related in cycles. No change stands out as a separate event; it is correlated with a similar event which has preceded it, and one that has followed or will follow it, from which it is separated by a dissimilar interval. Climate may thus be likened to a flowing stream which rises and falls in response to certain causes. It is not a series of detached events, but an organic whole in which each part bears some relation to the other parts. Considering climate as a continuous process, it follows that we must recognize changes or variations of climate only as phases or points of a particular climatic cycle, which lose their meaning and value unless they are considered in connection with the cycle itself. It is in this sense that changes and variations are spoken of in the following pages, where the cycle is regarded as the climatic unit."

Ignoring the familiar cycle of the year, there is more or less conclusive evidence of cycles of 2.5, 11, 22, 35, 50, 100, 400, and 1,000 years, approximately. In addition, there are the great geological cycles of unknown duration, which are discussed at some length in "Plant Succession" (337).

The 11-year cycle.—The best-known and most significant of climatic cycles for the present day is the 11-year cycle and its multiples. So far as its relation to tree growth, and hence to vegetation, is concerned, our knowledge of this cycle is due chiefly to Douglass (1909, 1914, 1919) though Huntington (1914) and Kapteyn (1914) have had a share in establishing the certainty of this relation. The effect of cycles upon succession, and consequently upon indicator communities and crop production, has been pointed out by Clements (1916:342; 1917:304; 1918:295). The relation of the 11-year cycle to changes in native vegetation and to variations in plant production has received constant study since 1914. It has proved so universal and fundamental as to warrant its being made the basic feature of production systems in the arid West (fig. 12).

The 11-year cycle is known also as the sun-spot climatic cycle, owing to the striking correspondence with the sun-spot period. The correlation of the dry and wet phases of climate and of the variations of tree growth with the sun-spot cycle is often so exact as to warrant the assumption of a causal relation between the two. Such a relation has not yet been established, how-

ever, and investigation at present is chiefly confined to the nature and extent of the coincidence between them. The outstanding fact is that our knowledge has reached a point where it seems increasingly possible to employ the sun-spot cycle as a method of anticipating the coincident or related changes in climate and vegetation.

Evidences.—The evidence of the cycle of sun-spots has all the certainty of astronomical data. The number of sun-spots has been recorded for every year since 1750, and the dates of the maxima and minima are definitely known as well as their intensity. Cycles in the annual growth of trees have been found by Douglass in a number of diverse regions, in Europe as well as America. It is obvious that trees growing in the most favorable conditions will not exhibit cycles, since there is no limiting factor to produce variations in the width of the rings. Moreover, the same tree sometimes fails to show cycles throughout its life, or does not show them with equal clearness. This is not difficult to understand when the complex relations of factors, of competition and reaction, parasites, fire, lumbering, and other disturbances are taken into account. By far the greater part of the evidence of existing cycles has been furnished by Douglass (1919). In his study of Arizona trees, he has found that, during the last 160 years, 10 of the 14 sun-spot maxima and minima have been followed about four years later by pronounced minima and maxima in tree-growth, and that the same trees show a strongly marked double-crested 11-year cycle during some 250 years of their early growth. They likewise exhibited a relation to the temperature curve for southern California, and this curve in turn resembled in form and phase the inverted curve of the sun-spot cycle.

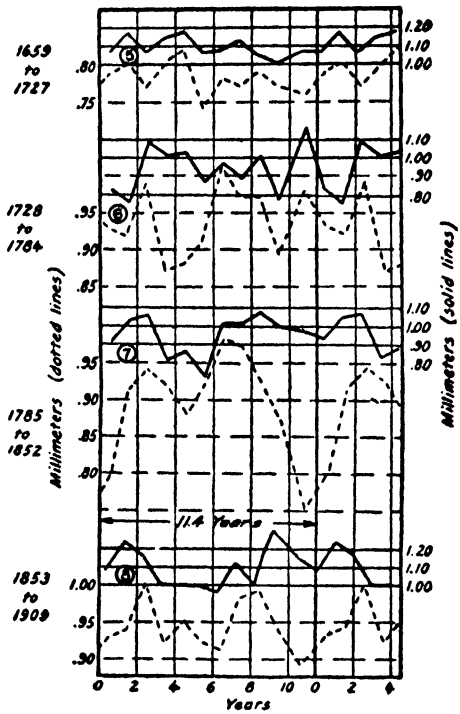


FIG. 12.—The 11-year cycle during the last 250 years, as shown by the yellow pine and *Sequoia*. After Douglass.

In the investigation of trees growing in wet climates, Douglass has also found conclusive evidence of cycles. The trees of Eberswalde near Berlin showed the 11-year sun-spot cycle since 1830 with accuracy. In the group as a whole, the agreement is marked, the maximum growth falling within 0.6 year of the sun-spot maximum. In six groups of trees from England, northern Germany, and the lower Scandinavian peninsula the growth since 1820 shows pronounced agreement with the sun-spot cycle, every maximum and minimum since that date appearing in the trees with an average variation of 20 per cent.

Kapteyn (1914:70) has studied the growth of oak trees in Holland and Germany and reaches the conclusion that during fairly long intervals of time they exhibit not only a regularity, but also an actual and fairly constant periodicity in growth. From 1659 to 1784, or for a stretch of 125 years, a period of about 12.4 years is clearly indicated. While this period disappears in certain groups, it persists in others, so that its recurrence for two centuries is demonstrated, with only one minimum missing. Huntington (1914:135) has devoted his attention chiefly to the major sun-spot cycles indicated in the rings of trees and has secured some exceedingly suggestive evidence of cycles of 100 years and more. Douglass (1919:111) has examined the trees studied by Huntington, in order to obtain evidence from them as to the shorter cycles, especially that of 11 years, and to carry the existence of such cycles back for a period of 3,200 years:

"The variations in the annual rings of individual trees over considerable areas exhibit such uniformity that the same rings can be identified in nearly every tree and the dates of their formation established with practical certainty.

"In dry climates the ring thicknesses are proportional to the rainfall with an accuracy of 70 per cent in recent years, and this accuracy presumably extends over centuries; an empirical formula can be made to express still more closely this relationship between tree growth and rainfall; the tree records therefore give us reliable indications of climatic cycles and of past climatic conditions.

"Certain areas of wet-climate trees in northern Europe give an admirable record of the sun-spot numbers and some American wet-climate trees give a similar record but with their maxima 1 to 3 years in advance of the solar maxima. It is possible to identify living trees giving this remarkable record and to ascertain the exact conditions under which they grow.

"Practically all the groups of trees investigated show the sun-spot cycle or its multiples; the solar cycle becomes more certain and accurate as the area of homogeneous region increases or the time of a tree record extends farther back; this suggests the possibility of determining the climatic and vegetational reaction to the solar cycle in different parts of the world.

"A most suggestive correlation exists in the dates of maxima and minima found in tree growth, rainfall, temperature, and solar phenomena. The prevalence of the solar cycle or its multiples, the greater accuracy as area or time are extended, and this correlation in dates point toward a physical connection between solar activity and terrestrial weather.

"The tree curves indicate a complex combination of short periods including a prominent cycle of about 2 years."

In addition, Douglass has made a preliminary study of sections of fossil trees, which show a similar cycle for some of the more recent geological periods.

Considerable preliminary work has been done in tracing the effects of the 11-year cycle in plants other than trees and in plant communities. It has been discovered that the dominant shrubs of sagebrush, chaparral, and desert scrub often show this cycle in the growth-rings and that, in some cases at least, the age of the shrub suggests that establishment takes place largely and sometimes only during the wet phase of the cycle. Studies of the extension of forest and woodland into grassland or other arid communities has shown that the entrance of the young trees occurred during the wet phase. Henry (1895:49) has shown that the height-growth of trees varies greatly from wet to dry periods, and it seems certain that a similar relation exists

for seed-production. In the special study of grazing during the past five years a large amount of material has been collected which shows the critical effect of the wet and dry phases upon growth and reproduction. As is well known, field crops also exhibit a striking response to years of abundant rainfall as well as to those of drought. While methods of tillage influence crop production profoundly, the latter clearly reflects the wet and dry phases of the climatic cycle at those stations in the arid regions where the record is sufficiently long. The effect of the 11-year cycle upon animals is most strikingly seen in the case of range cattle, which live under semi-natural conditions, but it is also readily discovered in all animal populations which are directly dependent upon the natural vegetation of arid regions for their food-supply.

Periods of drought.—While both wet and dry phases have a marked effect upon the annual production of natural and cultural crops, the periods of drought stand out with especial vividness. While this is particularly true of arid regions, it holds likewise for semi-arid ones during the period of early settlement, when economic resources are at a minimum. The consequences are sufficiently disastrous even in such cases, as the history of settlement in the Middle West proves. In the case of a native agricultural population held more or less rigidly within its own boundaries by the pressure of other tribes, they led to famine with attendant wars and revolts. As a result, there is much historical evidence of the periods of drought and famine in the Southwest, and this makes it possible to discover how closely these correspond with the phases of the 11-year cycle. As would be expected, there is frequent mention of droughts in the chronicles of Mexico and the Southwest from 1600 to 1850. A much smaller number of these were accompanied by famine, and appear to represent drought periods. Of more than a dozen such periods, all but two occurred at the sun-spot maximum, or within a year or two of it, and furnish a record of agreement comparable to that of the last half-century (fig. 13).

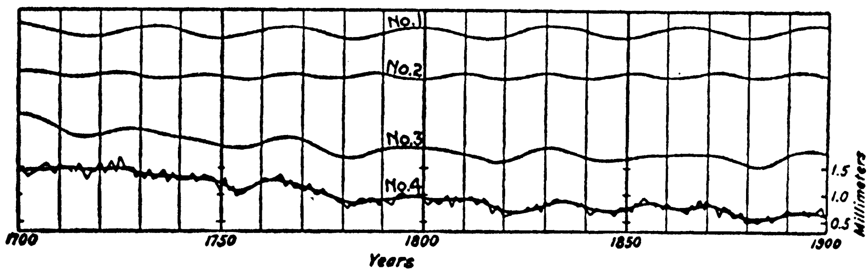


FIG. 13.—Double and triple sun-spot cycle in yellow pine from 1700 to 1900 A. D. After Douglass.

The agricultural development of the West began with the passage of the homestead act in 1862, and the consequent inrush of settlers. Since that time the drought periods are known with certainty, and their correlation can be made without question. In this connection it is essential to distinguish between drought periods and drought years. The former consist of two to three or even four years and are felt generally throughout the West. In the Great Basin, as well as in the Southwest, a single year of drought for a particular region or locality may occur at almost any time, since the normal rainfall is so

low that almost any deficit is equivalent to a drought of some degree. However, while a drought year involves inconvenience and loss, it rarely causes disaster and the general abandonment of recently settled regions. Hence, in the discussion of climatic cycles and drought, the latter is understood to be a drought period several years in length and extending over all or nearly all of the West.

Recurrence of drought periods.—The assumption that the 11-year cycle could be traced in the present and future as well as in the past (Clements 1916:330; 1917:304, 1918:295) led to a study of the coincidence of drought periods and sun-spot maxima from 1860 to 1915. The sun-spot maxima for this interval of 55 years occurred in 1860, 1870-72, 1883, 1893, and 1907. The maxima of 1870-72 and 1893 were known to coincide with times of general and critical drought in the West, and it was found that similar conditions had prevailed in 1859-60. In the case of the maximum for 1907, the deficit fell in 1908-09 for most regions and was less marked, while for the maximum of 1883 the record showed an excess of rainfall quite as often as a deficit. The close correspondence of sun-spot maxima and drought in 1870-72 and 1893-95, and the decrease or absence of agreement in 1883 and 1907, suggested that the maximum effects occurred in multiples of the 11-year period (Plant Succession, 336). The period involved in the two major droughts was 21 to 23 years, and this appeared to warrant the suggestion that a similar critical drought would recur in connection with the sun-spot maximum of 1917. The year 1915 proved to be exceptionally rainy, perhaps due to a lag of the effects expected at the sun-spot minimum in 1913, with the result that the ensuing drought period of 1916-18 appears to have been the most general and severe ever known in the West.

Drought periods not only bear a relation to the maximum of the sun-spot cycle, but also to periods of increased rainfall, with which they show a definite alternation. This alternation of dry and wet phases constitutes the climatic cycle which corresponds with the 11-year sun-spot cycle. As Douglass has found in the case of tree growth (1919), the drought period is much more marked, at least in its effects, and its rings are consequently used as basing points. The wet phase is related to the dry one in a cause-and-effect sequence, in accordance with which a deficit is followed within a year or two by an excess, or an excess by a deficit. While a preliminary investigation of this point indicates that it is the general rule, it is often obscured by local variations in the spatial distribution of rainfall. The wet phase likewise shows a correlation with the minimum of the sun-spot cycle, but it is usually less definite and striking than that of the dry phase. However, in a large number of localities representing different regions of the West, the rainfall at the sun-spot minimum is usually above the normal. It seems more or less probable that periods of excessive rainfall for 1 to 3 years occur on the second or third multiple of the 11-year cycle, and that they precede or follow a drought period as a rule.

The evidence that drought has occurred at frequent intervals during the past 300 years is conclusive. It is equally certain that drought periods have regularly alternated with wet ones, though these are naturally less frequently noted in the human record. Moreover, it must be recognized that the alter-

nation of dry and wet phases will be seen most clearly in the grassland climax of the prairies and plains, where the rainfall ranges between 15 and 30 inches. East of this, only the most intense droughts will be noted as such, and the minimum crop production is apt to occur in years of excessive rainfall. In the Southwest, where the rainfall is always low, the economic effects of drought may occur in almost any year when the distribution or timeliness of the rain is at fault. The existence of a climatic cycle coinciding with the sun-spot cycle, and consisting of a dry and a wet phase which falls respectively at the sun-spot maximum and minimum, appears to be established beyond a doubt by the work of Douglass, Huntington, and Kapteyn, as well as by the study of vegetation. Much more work is required to explain certain apparent exceptions and contradictions in widely divergent climates, but none of these seem to invalidate the general principle.

Significance of the sun-spot cycle.—The establishment of a cycle of relatively dry and wet periods with a usual length of 10 to 12 years is of paramount importance to the practice of agriculture, forestry, and grazing in the West. Since rainfall is the limiting factor over most of the region, a knowledge of what can be expected in the way of variation in rainfall and changes of climate will be of the greatest help. The most serious handicap to the proper agricultural development of the West lies in the almost universal misconception of climate and the nature of its changes. Much of this arises from the mistake of the earlier geographers in regarding the Missouri Valley as a part of the "Great American Desert." The rapid development of this region was sufficient proof that it had never been desert, but the persistence of the old idea could be reconciled with the facts only by the assumption that the rainfall had greatly increased as a result of cultivation. This impression that the rainfall was increasing was further strengthened by the luxuriant development of the tall-grasses as a consequence of the disappearance of the buffalo. This mistaken idea still persists over much of the West, where a marked and permanent increase in rainfall is confidently expected to follow settlement. This error has further serious consequences in that it leads to each drought period being regarded as the last, and consequently prevents the adoption of systems of settlement and management which will reckon with drought periods as certain to recur. Even where experience made it clear that droughts still occurred, the prejudice in favor of a changing climate, together with the general optimism and inertia of the pioneer, prevented the recognition of the patent fact. Moreover, during the disastrous drought of 1916-18, stockmen were often found who admitted that drought had occurred before and probably would again, but stated that this fact would be readily forgotten when the rains came.

The meteorologists have proved repeatedly, from the weather records, that there has been no progressive change in the climate of the West during the settlement of the latter. This has been conclusively shown by Swezey and Loveland (1896: 137) for Nebraska, the central position of which makes it typically representative of the climate and vegetation of the grassland climax:

"If we examine the precipitation for the series of years from 1849 to 1895 inclusive given in Appendix II, we shall find that, although the rainfall of the past few years has been less than that of the earlier years of the series, so far as we can judge from the rather meager records of those earlier years, yet

there is afforded no evidence of any considerable progressive change in the climate of the State, either toward wetter or drier conditions. There have been excessively wet and excessively dry years, the annual rainfall having ranged from 13.30 inches to 47.53 inches; there have been groups of wet years and groups of dry years succeeeding one another in a rather irregular manner. Thus the 47 years may be grouped into five periods as follows: The first 10 years were mostly wet years, only one of them, viz., 1852, having a rainfall less than normal; the next 9 years, 1859 to 1867 inclusive, constituted a period of scant rainfall, including particularly the exceedingly dry years of 1863 and 1864 and the scarcely less dry years of 1859 and 1860; the 9 years from 1868 to 1876 inclusive included years of plenteous and years of scant rainfall succeeding each other in a quite irregular manner; then followed 10 years, 1877 to 1886 inclusive, of rainfall generally above the normal; and finally the last 5 years have been, with the exception of 1891 and 1892, years of deficient rainfall, with the year 1894 the driest of the whole 47.

"But if we divide the entire series of 47 years into two periods of 24 and 23 years respectively, the average rainfall of the first period will exceed that of the last by only about an inch. The first year of the series, 1849, was one of excessive rainfall, not only as shown by the record made at Fort Kearney, the only station in Nebraska at which records were kept, but also as confirmed by records in the adjacent Territories. This difference of a little more than an inch between the mean rainfall of the first 24 years and that of the last 23 years of the 47 would almost disappear if this year of 1849 were omitted from the series; the mean precipitation for the 23 years from 1850 to 1872 is 23.55 inches, while that of the 23 years since is 23.46 inches.

"The conclusion, therefore, seems to be a safe one that the average rainfall of Nebraska, although subject to great fluctuations from year to year, yet in the long run remains substantially unchanged, so far as we can discover from the records of nearly half a century."

Prediction of drought periods.—The sun-spot cycle may furnish a ready method of predicting the occurrence of dry and wet periods. The sun-spot numbers are recorded with the greatest accuracy and detail, and the number for each month and year is readily obtainable. These numbers, taken in conjunction with the length of the recent cycles, make it possible to forecast the date on which the next maximum and minimum will fall, as well as something of their intensity. During the past century the average of 11.4 years for the cycle has been strikingly evident, practically all the cycles being from 10 to 12 years long. The accuracy of the correlation between the sun-spot cycle and the climatic cycle as recorded in the growth of trees is 85 per cent, according to Douglass's results (1919). This compares favorably with the accuracy of the daily forecasts of the Weather Bureau, and still more favorably with that of the weekly forecasts. However, there is one essential difference, in that the latter are actual forecasts, while the prediction of dry and wet phases has been attempted as yet only for the dry and wet phases of the current cycle (Clements, 1917, 1918). The close correspondence between the sun-spot cycle and the curve of tree growth strongly suggests a similar degree of accuracy in actual prediction, but repeated trial can alone determine this, as well as disclose the reasons for failure.

While it is thought and expected that the use of the sun-spot cycle will permit the prediction of drought periods for the West in general, as well as the occurrence of intervening but more diffuse wet periods, the prediction for

a particular locality is subject to more uncertainty. In this respect, cycle predictions resemble the daily and weekly weather forecasts. The failure of a relatively small number of these to be verified is due chiefly to changes of intensity or of pathway in the cyclonic area. In addition, there are more obscure local differences in evidence in almost every storm by which the amount of rain may vary greatly at two neighboring points. As Kullmer and Huntington have pointed out (1914), the shifting of the storm-belt seems to afford a causal explanation of climatic differences at the sun-spot maximum and minimum, as well as of variations from one locality or region to another. Thus, while drought periods are general for the West at the double sun-spot cycle, as in 1870-72, 1893-95, and 1916-18, not all regions showed 3 years of drought, and during any one year a few regions recorded a rainfall approaching normal. Naturally, the drought was most intense and prolonged in the areas of normally scanty rainfall, and it decreased more or less regularly in the direction of regions of medium precipitation. During such periods, it is even possible that high mountain regions may receive an excessive amount of rain. This seems to result from the principle of compensation, in accordance with which deficit and excess are regularly linked together in time or in space. For the present, this is regarded as the most plausible explanation of variations and inconsistencies in the behavior of the climatic cycle, but it is probable that further knowledge will show that these are connected with the differentiation of contiguous climates. Hence, while the method of cycles can not assume to forecast the number of inches of rain for any locality during a certain year, it can predict the recurrence of drought periods and of succeeding wetter years for the West in general. The drought period will concern three regions out of four during most of its duration, and it will affect practically every locality at some time during its phase.

Utilization of cycles.—A study of settlement in the West since 1865 reveals the fact that it corresponds more or less closely to the climatic cycle. The exceptions are afforded by the rapid inrush after the homestead act, the Kinkaid act, etc., or after the opening of new regions. The general movement of settlers has advanced and receded in almost perfect agreement with the wet phases and drought periods of the climatic cycle (cf. Brückner, Huntington 1914: 89). A few years of unusual rainfall have afforded unscrupulous real estate dealers and immigration commissioners an opportunity to dispose of even the most worthless land. The ensuing drought period then led to crop failure and the wholesale abandonment of the region, to be followed by another influx of settlers during the next wet phase. In more than one region of the West this process has been repeated three or four times, and its disastrous operation will continue until the States and the National Government recognize the necessity of proper land classification and of adequate regulation of settlement.

The knowledge that drought periods will recur is indispensable to any accurate and successful classification of land and to the economic management of dry-farm, grazing range, or forest. These results, which are of the first importance for the West, do not depend necessarily upon the accuracy of predictions based upon the sun-spot cycle. They are clearly indicated by the actual experience of the last 60 years, which not only confirms the recurrence of drought periods, but also suggests the interval. However, it is clear that

it would be of the greatest value to be able to forecast the date, duration, and intensity of each drought period with some accuracy, as well as to anticipate the increasing rainfall of the wet phase. This would not only permit the taking of the necessary precautions against the disasters due to drought, but it would also make possible the development of an optimum system of management. This would enable the farmer to fit his crops and methods of tillage to the variations in rainfall and would permit the stockman to increase or decrease his herds or to vary his supplies of forage with the wet and dry phases of the cycle. In short, the cycle management of all the basic practices of the West would provide the maximum insurance against loss or disaster and would afford the greatest possible annual returns. It is further discussed in connection with agricultural and forest indicators, but its value is especially emphasized under grazing, since the latter and the related dry-farming are most dependent upon climatic conditions.

FARMING INDICATORS.

Types of farming.—With reference to indicators, types of farming may be based upon conditions or upon crops. Since the former determines the methods and return (and often the crop as well), it seems to afford the better basis. Accordingly, the usual division into humid and arid farming is employed here, with a further division of the latter into dry-farming and irrigation farming. It is clear that no sharp line exists between the types of agriculture in humid and arid regions. Between the two lies a broad belt of semi-arid country in which there is a gradual adjustment of methods and crops to increasingly arid conditions. The distinction is further obscured by the variation in rainfall from the wet to the dry phase of the climatic cycle. During the wet period humid farming is possible through most or all of the semi-arid belt and the need of drainage becomes felt over a much wider area. During the dry period arid conditions are pushed across much of the semi-arid country and semi-arid conditions develop in the outlying humid areas. However, practices change much less than conditions; the general area of the humid, semi-arid, and arid regions remains essentially the same, with their mutual relations identical.

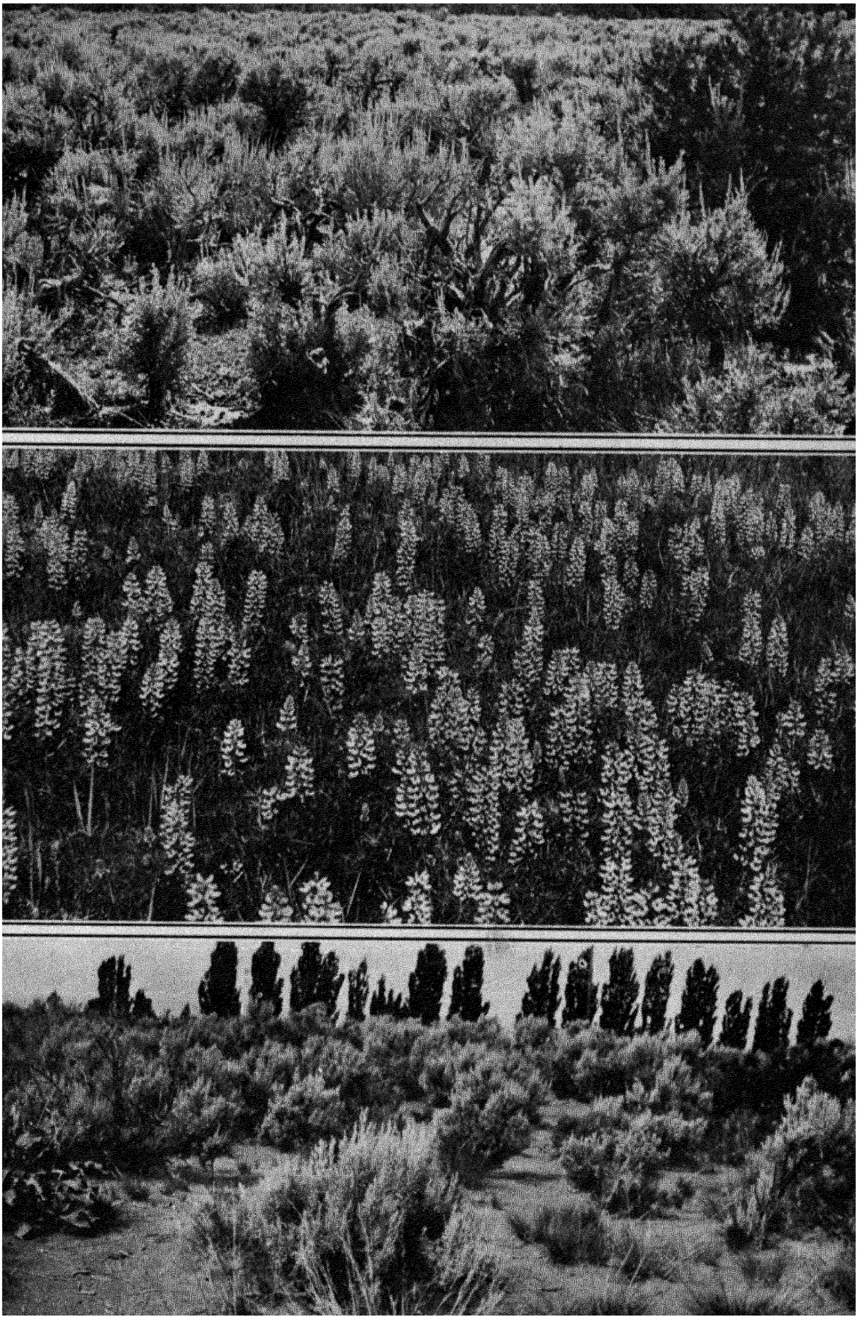
The humid region is regarded as possessing a lower limit of 25 inches of rainfall, while the semi-arid has a range of 15 to 25 inches, and the arid from 2 to 15 inches. As would be expected from variations in the annual amount and distribution of the rainfall, semi-arid areas with 20 to 25 inches of rain are characterized by the humid type of farming, and those with 15 to 20 inches by dry-farming. The latter type usually reaches its lower limit at 12 inches, or at 10 inches where the rainfall is largely of the winter type. Below 10 inches, farming is profitable only by means of irrigation. Naturally, the latter is also extensively practiced in regions with 10 to 20 inches of rain, and to some degree under even higher rainfall. As Briggs and Belz (1911) have shown, the efficiency of rainfall depends upon the amount of evaporation, and hence decreases more or less regularly from the northeast to the southwest in the western United States.

Relation of types of farming to indicators.—Because of the control made possible by irrigation, methods of tillage, and variation in crop or variety, indicator values are less definite in the case of types of farming than in graz-

ing or forestry. Their significance is further reduced by the possibility of irrigation and by such economic considerations as markets and transportation. Moreover, the method of conserving water-content by means of summer fallow enables dry-farming to be practiced in regions where otherwise irrigation would be the only successful method. On the other hand, where annual cropping is the rule, dry-farming methods pass imperceptibly into those of ordinary farming with good tillage in semi-arid and subhumid regions. In spite of this, there is a general correspondence between climax associations and types of farminig. The tall-grass prairies are typical of regions in which humid farming prevails. The mixed prairies and short-grass plains denote country in which dry-farming of the annual crop type is more or less successful. The bunch-grass prairies and desert plains characterize regions of scantier rainfall, for the most part of the winter type, and hence are chiefly to be correlated with dry-farming by means of summer fallow. Subclimax sagebrush has practically the same indicator value as the associated grasses. When these are tall-grasses the indications are of dry-farming with annual cropping, and when they are bunch-grasses they indicate summer fallow methods. Climax sagebrush is also an indicator of the latter when the rainfall does not fall below 10 inches. Over the major portion of the central Great Basin, sagebrush indicates a climate in which crop production is impossible without irrigation. This is likewise true of practically the whole desert scrub climax except for small areas at higher altitudes or near its eastern limit, where it approaches or mixes with the grassland. The indications of chaparral are variable. While they are largely non-agricultural, chaparral resembles scrub generally in its indication of dry-farming or irrigation practices, as is true also of woodland where soil and topography are favorable. Montane forest usually receives enough rainfall to make humid farming possible, though both dry-farming and irrigation are practiced in the lower yellow-pine belt. Most of the montane zone lies above the limit of profitable agriculture, and the occasional fields of hardy cereals are restricted to the warmer valleys and lower slopes (plates 31 and 32).

Edaphic indicators of types of farming.—These are more local and hence less important than the climatic indicators just discussed. They are primarily related to soil and water-content, and consequently are of the greatest service in regions with marked soil characteristics, such as sandhills, bad lands, saline basins, or in river or lake valleys with relatively high water-content. The same farm may have lowland and upland areas, or may show considerable variations in soil with corresponding indications as to types of farming. This is particularly true of the wet valleys in the sandhills of Nebraska and of the many river valleys with a generally westward direction in Nebraska and Kansas. The wet valleys are marked by meadow communities, and many of them are susceptible of farming by the usual methods. The river valleys are occupied by similar communities of which *Andropogon*, *Agropyrum*, *Calamovilfa*, *Elymus*, or *Spartina* are the dominants, or they may be characterized by the presence of scrub. In either case the indications are for subhumid farming, especially during the wet period of the climatic cycle.

Shantz (1911: 85) has pointed out the agricultural significance of the difference between lighter and heavier soils in passing to the westward. The



A. Tall valley sagebrush indicating a deep soil for irrigation farming, Garland, Colorado.
B. A legume, *Lupinus plattensis,* indicating a rich moist soil, Monroe Cañon, Pine Ridge, Nebraska.
C. Relict *Stipa* and *Balsamorhiza* in sagebrush, indicating a bunch-grass climate for dry-farming, Hagerman, Idaho.

lighter soils conserve water to a much larger degree, and hence require less intensive methods of cultivation than do the heavier ones. In some regions, and especially during certain years, this may amount to ordinary cropping on one and dry-farming on the other. Kearney and others (1914:416) have shown that sagebrush (*Artemisia tridentata*) is an indicator of both dry-farming and irrigation farming in Utah when it makes a good stand and vigorous growth. Communities of *Kochia vestita* or *Atriplex confertifolia* generally indicate the necessity of irrigation to rid the soil of the excess of salts. The mixed community of *Sarcobatus* and *Atriplex* has essentially the same significance, though it indicates the desirability of drainage as well. Hilgard (1906:536) regards *Sporobolus airoides, Spirostachys, Salicornia, Suaeda, Sarcobatus, Frankenia, Cressa,* and *Distichlis* as indicators of the necessity of underdrainage as a prerequisite to successful irrigation farming.

CROP INDICATORS.

Nature and kinds.—While the factor-complex must always be kept in mind in the correlation of indicator communities and crops, water is the paramount factor practically throughout the West. The importance of temperature as a direct factor increases with latitude and especially with altitude, but it is regularly less than that of water. The water relations are primarily a question of rainfall and evaporation, more or less modified locally by topography and soil. As a consequence, it is desirable to distinguish climatic and edaphic indicators of crops. The former denote the general climatic regions for particular kinds or varieties of crops, the latter the soil or topographic differences which break up the climatic uniformity of a particular region and render other kinds or varieties preferable. Climatic indicators are primarily climax communities of varying rank, while edaphic indicators are mostly seral or developmental communities. Crop indicators may serve to denote (1) the type of crop, as grain or forage; (2) the species in a general sense, as wheat, oats, or rye; (3) the kind, as winter and spring, or hard and soft wheat; and (4) the variety, such as Marquis, Fife, or Preston. They also permit correlations with differences in methods of practice, such as dry-farming with and without summer tillage, etc.

Little use has been made of plant communities as indicators of the type or kind of crop. This has been a natural outcome of the enormous amount of crop experimentation carried on by the Department of Agriculture and the various State experiment stations during the past two decades. Nearly 100 stations and substations have been concerned in this work, and it is a logical conclusion that they have made the use of crop indicators unnecessary. It seems, however, that the very extent and thoroughness of the experiments with various crops must increase the accuracy and readiness with which indicators can be used. In spite of the numerous stations, there are many large regions still unrepresented. In addition, the climatic gradations and edaphic variations are so numerous that the native vegetation alone affords an adequate method of taking them all into account. As a consequence, the opportunity for working out a general system of crop indicators seems exceptionally good. This would be based upon the correlations between native communities found about each station and the types and kinds of crops demonstrated to be the most desirable for that region. While such correlations

can be obtained from the results of practically all stations, the investigations carried on at those of the Office of Dry-Land Agriculture are of the greatest value. This is due to a number of causes, chief among which are the use of the same crops and methods, the wide extent of the studies, the large number of stations in a single great climax, the grassland, the more or less gradual decrease in rainfall to the westward, and the consequent readiness and accuracy with which comparative results can be obtained. The correlations discussed below have been based chiefly upon the results obtained by this Office, supplemented for the more or less representative central portion by the studies made at the experiment stations of Nebraska and Kansas. In all of them, it should be borne in mind that the correlation and the corresponding indicator community have the greatest accuracy in the region of the particular station or stations, and that this value decreases more or less regularly in the direction of stations with different correlations. However, the practical usefulness of the indicator increases with the remoteness from a particular station, providing always that the plant community remains the same, since the latter indicates that the conditions are essentially unchanged.

Climatic indicators of the types of crops.—The correlations considered here are based upon the fact that crops, like natural dominants, have an area of maximum production about which they shade out in all directions. This diminution is generally less marked in the case of crops, owing to the modifying influence of culture as well as of economic factors. Corn affords the most striking example of a crop grown throughout an extensive region, but with a well-defined area of maximum production. As a crop it extends over the major portion of several climaxes, but its optimum area, the "corn belt," is more or less clearly limited. The limits of this belt fall within the main area of the subclimax and true prairies, which are to be regarded as the indicators of maximum corn production. In this connection, it is at least suggestive that four of the dominants of these communities belong to the genus *Andropogon,* which systematically and ecologically resembles corn more closely than do any of the other grassland dominants. As might be expected, wheat exhibits an even more extensive correlation with the grassland. The region of maximum production is from Saskatchewan to Oklahoma, with secondary maxima in Indiana and Illinois, and in Washington and Oregon. The maximum falls almost wholly within the region occupied by the true and mixed prairies. Here also it is perhaps significant that *Agropyrum,* with its close relationship to *Triticum,* is an important dominant in these communities and is the major dominant in the great wheat region of the Palouse. Oats show a somewhat similar relation to grassland, as does barley, but rye manifests no clear correlation. On the whole, however, there is good evidence for regarding grassland made up of tall-grasses as the primary indicator for the optimum production of cereals (cf. Smith, Baker and Hainsworth, 1916; Waller, 1918).

Hay and forage crops generally are more or less evenly distributed through the deciduous forest and grassland climaxes, but there is a clear regional differentiation in the case of alfalfa and sorghums. The chief center for alfalfa is in central Nebraska, Kansas, and Oklahoma, with local centers in the main irrigated sections of the West, practically all of which occur in grassland or sagebrush. The sorghums, whether grown exclusively for fodder or for grain as well, have their center of maximum production in western Kansas,

Oklahoma, Texas, and eastern New Mexico. It corresponds closely with the eastern half of the short-grass associes, in which *Bulbilis* and *Bouteloua gracilis* are the dominants. Cotton reaches its maximum in a well-marked region which corresponds with the southern forest, except in central Texas and Oklahoma. Under irrigation it promises to develop a secondary center for long-staple varieties in the desert scrub climax of the Southwest. Of the other types of crops, vegetables are more or less evenly distributed over the eastern half of the country, with marked regional differentiation for certain kinds and many local foci. Fruits and nuts show a similar uniform distribution in the East, but they are almost wholly confined to the forested region and its extension into the southeastern prairies. This correlation is wholly to be expected on the basis of similarity in life-form. The most important fruit districts of the West lie in the sagebrush and grassland climaxes and depend upon irrigation, as the difference in the life-forms indicates.

Climatic indicators of kinds of crops.—The correlation of the kind of crop with indicator communities has already been touched upon. It is often less definite than with types of crops, but there are a number of correspondences of much interest and value. These are perhaps best shown by the three kinds of wheat, namely, winter, spring, and durum. Winter wheat has its center in the true prairies of Kansas and Nebraska, in which *Andropogon* plays an important part. Spring wheat and durum reach their best development in the mixed prairies or in the northern portion of the true prairies, where *Stipa spartea* and *Agropyrum glaucum* are especially important. They are more or less equal in value in the eastern portion of the true prairies, but durum shows an increasing advantage to the west, and is superior to spring wheat practically throughout the mixed prairies. In the bunch-grass prairies of the Northwest the advantage is reversed, and spring wheat outyields durum. The general use of summer tillage in connection with the winter precipitation favors winter wheat because of its earlier period of growth.

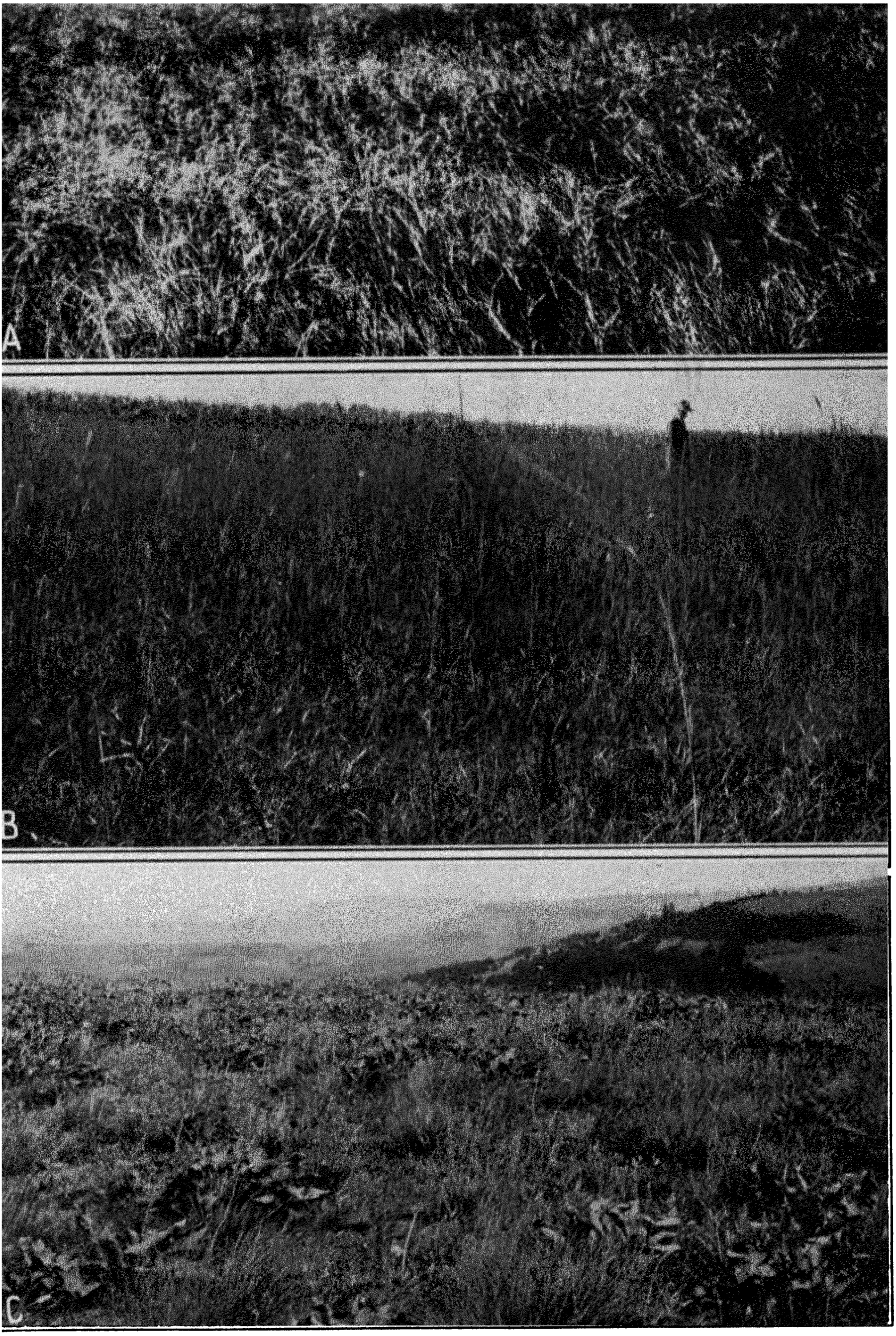
The region of the maximum production of barley comprises the northern half of the true prairies, while that of oats includes the major portion of both the subclimax and true prairies. Flax finds its maximum in the transition from the true to the mixed prairies, but it is extending more and more into the latter in western North Dakota. While there is a marked correlation between the sorghums as a group and the short-grass plains and their transition to the tall-grasses, the various kinds of sorghums show no clear correlations with indicator communities. This is perhaps due in some measure to the relatively short period of trial, but probably results chiefly from the fact that qualities of earliness and dwarfness are more significant than the group differences (Ball, 1911; Ball and Rothgeb, 1918: 88). In contrast with the grain-sorghums, the sorgos show an increasing correlation with the tall-grasses, and in western Nebraska and the Dakotas are to be related to the mixed prairies.

Climatic indicators of varieties.—The significant correlation of indicator plants with varieties is naturally more difficult and less satisfactory than in the case of types and kinds of crops. This is largely because the differences between varieties can be modified or reversed by seasonal variations or cultural methods, as well as by the complex of local conditions. It is also due in part to the fact that the minor differences in indicator communities arising

from varying grouping of the dominants and from changes in the subdominants have received little careful study. In spite of these facts, there are certain obvious correlations where varieties differ in some clear-cut quality, such as earliness or dwarfness. Both of these are related to the evasion of drought or frost, and can be correlated in some measure with indicators of changing altitude or latitude, or with decreasing rainfall. It should be borne in mind also that each variety primarily represents a certain degree of adjustment to particular conditions, and that some of them are certain to be replaced by other varieties as a result of longer trial or changing demands.

Wheat exhibits the best indicator correlations with varieties because of its greater differentiation and wider area. Among the durum wheats, Arnautka is indicated as the best variety by the true prairies with greater rainfall and shorter season. Of the spring wheats, Preston is generally indicated by true prairie, Marquis by mixed, and Bart by the bunch-grass prairie. Winter wheats are less clearly indicated owing to their greater drought evasion, but the Turkey and Kharkof are the principal varieties in the true prairies, and various strains of Crimean in the short-grass plains and the sagebrush. The soft winter wheats correspond with the subclimax prairies more or less nearly, while the hard varieties correspond with the true prairies and short-grass plains, which are relatively drier and colder. The varieties of oats show a fair degree of correspondence with the grassland associations. Kherson generally gives the best yields in the true prairie, Burt in the short-grass association, 60-day in the mixed prairie, and 60-day or Kherson in the bunch-grass prairie. In Kansas, Blackhull kafir is the best variety in the subclimax and true prairies, Pink kafir in the broad transition to the short-grass, and Dwarf Blackhull in the short-grass proper, where it enters into competition with Dwarf milo and feterita. Orange sorgo is correlated with the subclimax and true prairies, and Red Amber with the transition and the short-grass plains.

Life zones and crop zones.—Merriam's classic paper upon the life zones and crop zones of the United States recognized seven divisions, the Arctic-Alpine, Hudsonian, Canadian, Transition, Upper Austral, Lower Austral, and Tropical (1898: 18; 1890: 18). The most important of these were subdivided into faunal areas, of which the Arid Transition, Pacific Coast Transition, Upper Sonoran, and Lower Sonoran are the ones found chiefly in the West. Lists of crops and their varieties were given for each of the areas and the zone ranges of crops were indicated by tables. These represented the most important correlations and were undoubtedly of value as a record of the results of experience and experiment up to 1898, though naturally many of the varieties have since been superseded. Many of these correlations were necessarily the same as for indicator communities in the same regions. Since the basis of Merriam's work was floristic and faunistic rather than ecological, the correlations were for the most part more general and less accurate. As has been indicated earlier, this was a necessary outcome of regarding temperature and fauna as the primary bases for such correlations rather than water and vegetation. One interesting consequence was the much greater use made of perennial crops, particularly the fruits, since these are naturally more subject to unfavorable temperatures than the annual ones. The need for a finer division of the faunal areas is well illustrated by the Upper Sonoran, which includes the grassland, sagebrush, chaparral, and woodland cli-



A. Mixed prairie (*Stipa comata*) indicating dry-farming, Scenic, South Dakota.
B. Tall-grass (*Andropogon furcatus*) indicating humid farming, Madison, Nebraska.
C. Bunch-grass prairie (*Agropyrum-Festuca*) indicating dry-farming with winter rainfall, The Dalles, Oregon.

maxes. The difficulty of correlating crops with such an extensive and varied area is mentioned by Cary in his discussion of this zone in Colorado (1911: 30):

"The distribution of Upper Sonoran crops is at present local; and so dependent are many of the crops upon natural protection, adequate water supply, and suitable soils, entirely aside from temperature, that they can not be grown over the whole of a region so varied as the Upper Sonoran of Colorado."

Whatever may be the shortcomings of the life-zone concept, they are more or less inevitable in a pioneer work covering such a vast field. With Hilgard and Chamberlin, Merriam must be given great credit for having recognized the value of natural indicators so early, and for pointing out many of the major correlations. His method has formed the basis for the surveys of Western States made by the Bureau of Biological Survey during the past 15 years. The first of these was that of Texas, made by Bailey (1905), in which little attention was given to crop correlations. In a similar study of New Mexico (1913; cf. Wooton, 1912: 10) he has discussed the crops of the Lower and Upper Sonoran zones in some detail, especially as to the fruits (23, 38). Cockerell (1897) was the first to give a general discussion of the life zones of New Mexico, as well as the first to make use of insects as zone indicators. Cary (1911: 29, 40) has dealt with the agricultural importance of the Upper Sonoran and Transition zones in Colorado. He has also characterized briefly the agriculture of the same zones in Wyoming (1917: 30, 39) and has pointed out the economic importance of the boreal zones (52). Robbins (1917) has described briefly the native plant communities in Colorado with especial reference to altitude and has discussed the general agricultural relations of the grassland, sagebrush, chaparral, woodland, and montane forest.

Edaphic indicators of crops and methods.—Variation in crop possibilities within a climate, due to edaphic or soil conditions, may be regional or local. Regional and local variations are both caused chiefly by variations in water-content arising from differences in soil, solutes, or topography, and the only important difference between them is that the one determines the general agricultural practice of a region, and the other that of a neighborhood or of a single farm. The responses of plants to local differences in water-content are readily seen, and the corresponding edaphic indicators are of much value in suggesting desirable or necessary local variations in crops or methods. Since practically all such local differences have to do with water-content or temperature, their indicators have the same general significance as in the case of the more general climatic differences. Such local variations in conditions may often be quite as great as those between adjacent climatic regions and edaphic indicators may consequently denote differences in crops and methods quite as great as climatic ones do. Since the number of such indicators is legion, and every small difference of soil or topography has a corresponding indicator, the adjustment of crop and method to any particular variation in conditions is largely a matter of practicability. Locally as well as generally, the chief differences in soil are represented by saline soil, hard land or gumbo, and sand. All of these have their proper indicators, as is well known, and it is only necessary to recognize that their local occurrence has much the same significance assigned to them by Hilgard, Shantz, Kearney and others for

more extensive regions. This is particularly well illustrated in the case of dune-sands, which are found in sandhill areas through the prairies and plains. It is best seen in the great sandhill region of Nebraska, where soil and topography have combined to present an unusual set of conditions. The loose sandy soil, lack of humus, and the maze of steep hills with intervening wet and dry valleys constitute a complex of factors marked by distinctive indicators and demanding a specialized type of agriculture (Cowan, 1916: 5). Such a region not only requires different methods and crops from those of the general climatic area, but the varying areas of wet valleys, dry valleys, and hillsides demand corresponding differences in treatment.

Indicators of native or ruderal forage crops.—The detailed study of secondary seres in fallow fields and similar disturbed areas has revealed a number of species of native herbs and weeds which give more or less promise as forage crops. During the three years of drought from 1916 to 1918, particular attention has been directed to those which made a vigorous growth or a good stand in fields in which forage crops were a failure, or in areas adjacent to such crops. A considerable number of weeds of much promise has been observed over an extensive region, and in addition a number of native species have been suggested as of possible forage value by their behavior during drought. By far the most valuable are *Melilotus alba, Helianthus annuus,* and *Salsola kali.* The former is rapidly taking its place as a forage crop in some regions and there seems little doubt that it will ultimately be grown as a dry crop over a wide area. *Helianthus annuus* has but recently been tested under field conditions (Arnett, 1917), but the results agree with the evidence in nature to the effect that it is of much value in dry regions, and especially during drought years. *Salsola* has been grown scarcely at all as a crop, but it has been cut as a weed crop and utilized as hay of a fair quality at least. While its tonnage is less than that of sunflower, it will often grow luxuriantly in places where the latter will not. This is true also of *Helianthus petiolaris,* which may be regarded as a dwarf native form of the common sunflower. The other coarse weeds whose behavior indicates that they will be found to have some forage value are *Chenopodium album, Amarantus retroflexus, A. hybridus, Erigeron canadensis, Iva xanthifolia, I. axillaris,* and *Brassica nigra.* The native species of weedy habit and of such vigorous growth as to suggest the probability of forage value are *Amarantus palmeri, A. powellii, A. torreyi, A. wrightii, A. fimbriatus, Acnida tamariscina, Psoralea lanceolata, Franseria tenuifolia, F. discolor, Atriplex rosea, A. expansa, Corispermum hyssopifolium,* and *Cycloloma platyphyllum.* The last four are adapted to saline soils, and the last two to sandhill areas as well.

AGRICULTURAL PRACTICE AND CLIMATIC CYCLES.

Cycles of production.—The close dependence of annual crops upon seasonal and annual rainfall makes it clear that they will reflect the various climatic cycles in some degree. The correlation is less exact than with the natural perennial crops of grasses, shrubs, and trees, owing to the effect of cultural methods and the choice as to times of planting. It is also more or less obscured by rotation and by changes of variety and method such as are constantly taking place in ordinary practice. Moreover, it may be completely destroyed for a particular year by hot winds of a few days' duration if they

occur at a critical period, such as that of the tasseling of corn. In addition, the correlation of cycles, rainfall, and crop production is most in evidence in a region such as the prairies and plains, where the rainfall is moderate, ranging for the most part from 15 to 30 inches. Above 30 inches the compensating effect of accumulated water-content tends to minimize the consequences of drought, while below 15 inches the margin of safety is so small that it is easily destroyed by local or incidental causes.

The evidence of definite cycles in crop production is difficult to obtain for the further reason that accurate records in a particular place for a long period are extremely rare. Few of these extend through a sun-spot cycle of 10 to 12 years, and practically none through the more significant double cycle of 21 to 23 years. However, the drought periods of 1870-72, 1893-95, and 1916-18 were so intense that a corresponding production cycle is shown in the crop averages for the regions concerned. The sun-spot maximum of 1907 marked a minor drought period which in most regions reached its culmination two or three years later. This discrepancy seems to be explained, in part at least, by the interference of a shorter cycle, probably the pleion or quarter cycle of 2.5 years, and by the action of the excess-deficit balance. Arctowski (1912: 745) has shown the relation of the corn crop by States and regions to the interaction of these two cycles. He has found not only that areas of excess and deficit in production bear a definite relation to each other, but also that this relation is preserved as they shift about from year to year. Douglass (1919: 106) has found that the 2.5-year cycle is regularly present in the growth of trees. Hence, it seems probable that the major cycle of crop production is the double sun-spot cycle of 21 to 23 years, and that this is made up of smaller cycles resulting from the interaction of the sun-spot cycle of 11 years and the quarter cycle of 2.5 years. Intensive research alone can determine how distinct and universal these may be. At present, it must be admitted that they are often much disturbed by the compensating action which follows an excess or deficit of rainfall. This is termed the excess-deficit balance, and is itself a short-period cycle, based apparently upon the fundamental physical correlation of action and reaction. Since it is usually 2 to 3 years in length, it is not improbable that it may be the 2.5-year cycle heightened by spatial variations in rainfall (fig. 14).

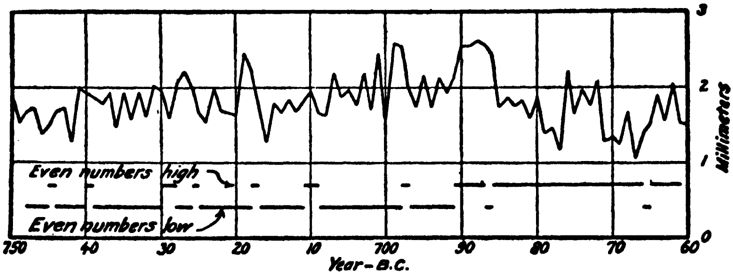


FIG. 14.—2-year cycle in a *Sequoia*. After Douglass.

An analysis of the production of grain-sorghums at Amarillo from 1907 to 1918 has been made to illustrate the possible relation to the various cycles. This has been drawn from the results of Ball and Rothgeb (1918), but is limited to the production in bushels of grain, as representing the more com-

plete response of the plant to growing conditions. The seasonal rainfall has been reckoned for the five months beginning with April and ending with August.

Rainfall and the production of grain-sorghums.

Year.	Annual rainfall.	Seasonal rainfall.	Milo.	Dwarf milo.	White durra.	Durra kafir.	Black-hull.	Dawn kafir.	Red kafir.	Brown kao-liang.
1907	18.09	11.90	....	....	....	....	....	....	....	....
1908	19.05	15.33	35	41	33	33	34	29	33	31
1909	19.59	10.80	6	11	12	4	6	14	5	11
1910	11.15	10.00	18	19	10	12	3	9	5	10
1911	22.73	15.66	32	38	29	30	19	40	19	22
1912	14.33	8.76	19	23	17	7	4	10	4	12
1913	18.97	7.90	0	0	0	0	0	0	0	0
1914	19.18	10.17	11	27	22	15	10	15	15	17
1915	27.65	17.78	61	68	37	28	60	53	51	85
1916	16.43	9.54	7	7	5	4	0	4	1	4
1917[1]	17.06	12.88	13	22	11	5	5	5	2	8
1918	18.11	8.73	7	10	0	3	0	1	0	2

[1]Unpublished data from the Office of Cereal Investigations, Bureau of Plant Industry, U. S. Department of Agriculture.

Ball and Rothgeb (1918: 22) have given a very instructive account of the distribution and timeliness of the rainfall of the various years in relation to yield. Their discussion makes clear the number of apparently chance factors which enter into the production of a crop. In spite of this, however, both the 11-year and the 2 to 3 year cycle can be recognized in the production as well

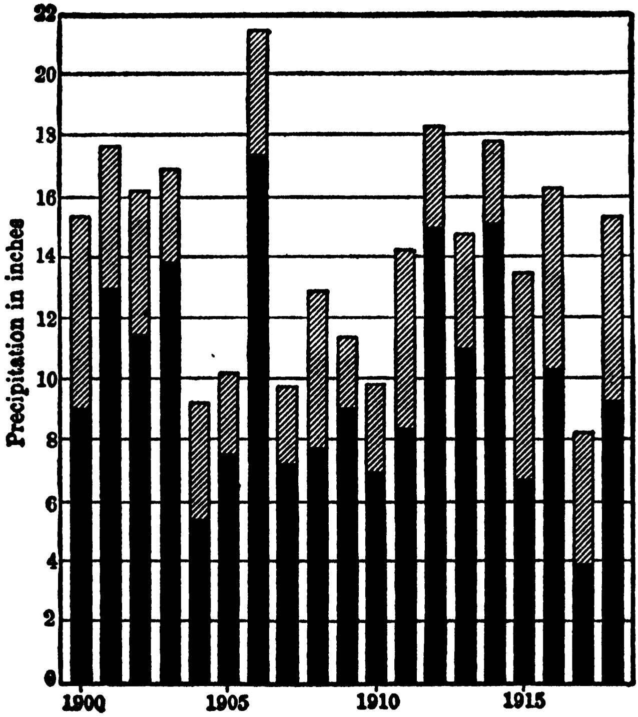


FIG. 15.—Graph of total and seasonal rainfall at Williston, North Dakota.

as in the rainfall. As seems to be the rule, these show more clearly in the summer than in the winter rainfall, and hence more clearly than in the annual rainfall. There is a tendency to maximum rainfall about the sun-spot minimum of 1913, and to minimum rainfall about the sun-spot maximum of 1918. However, it is much less decisive at Amarillo than at other places in the Great Plains, indicating the action of a spatial balance in the rainfall of a particular year. The evidence of the excess-deficit cycle of 2 to 3 years is much clearer. From 1908 to 1911 and 1911 to 1914, the cycle was 3 years, while from 1915 to 1916 and 1917 to 1918, it was 2 years. This is reflected in the production, the maximum yields occurring in 1908, 1911, 1915, and 1917. The yield does not correspond with either the annual or seasonal rainfall alone, though it follows the latter more closely. This is due to the fact that while the grains are like the grasses in being chiefly dependent upon the summer rainfall, they also show the effects of a water-content surplus or deficit arising from the year before. There can be little question that the water-content of the soil shows cycles corresponding closely to those of rainfall, and that scientific agriculture must come to take these into account in connection with forecasting the kind of crop and the yield for any particular year. Thus, while the investigation of rainfall and crop cycles presents many complexities, it appears that these are all worked out on the basic pattern of the 22-year, 11-year, and 2 to 3 year cycles. If this proves to be the case as

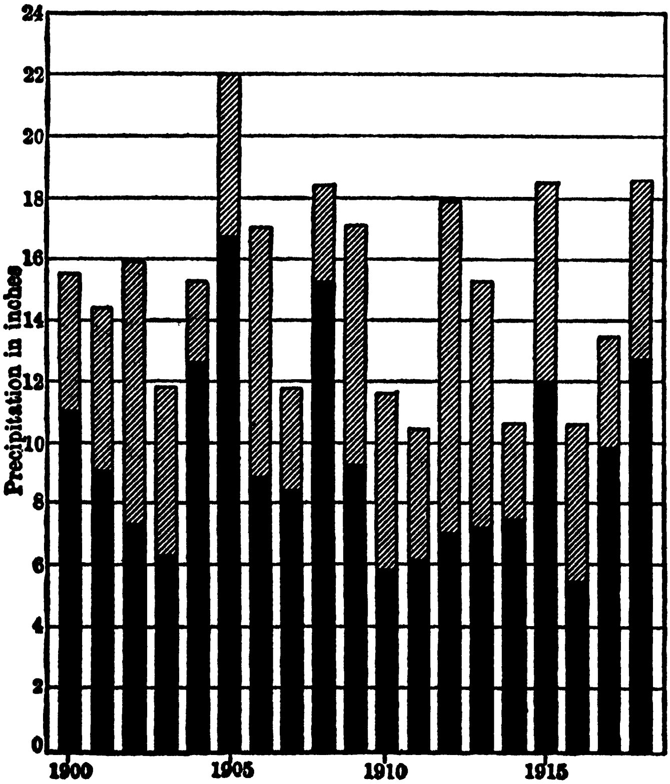


FIG. 16.—Graph of total and seasonal rainfall at Cheyenne, Wyoming.

the result of intensive studies throughout the West, it is probable that annual crop production may ultimately be forecasted with something of the accuracy of daily weather forecasts at present.

The excess-deficit balance.—The fact has already been emphasized that an excess of rainfall in one year is almost certain to be balanced by a deficit in the next year, while a great excess is often followed by two or rarely three years of deficit. As a rule ,an excess is an amount above the normal rainfall and a deficit is an amount below it. Moreover, an excess in one region is often counterbalanced by a deficit in another, or an increase or decrease in one region is not met by a corresponding change in an adjacent one. When the balance operates from one year to another, it produces a cycle of 2 to 3 years. This cycle exhibits marked variations in rainfall, so much so that it may obscure the normal effect of the 11-year cycle at its maximum or minimum, though apparently not that of the 22-year cycle. In order to illustrate the operation of the excess-deficit cycle, use has been made of columnar graphs of the rainfall at widely separated points in the grassland climax. The points selected are Williston (North Dakota), Cheyenne (Wyoming), Akron (Colorado), and Amarillo (Texas). In the case of the first three places, the graphs have been adapted from those prepared respectively by Babcock (1915: 5),

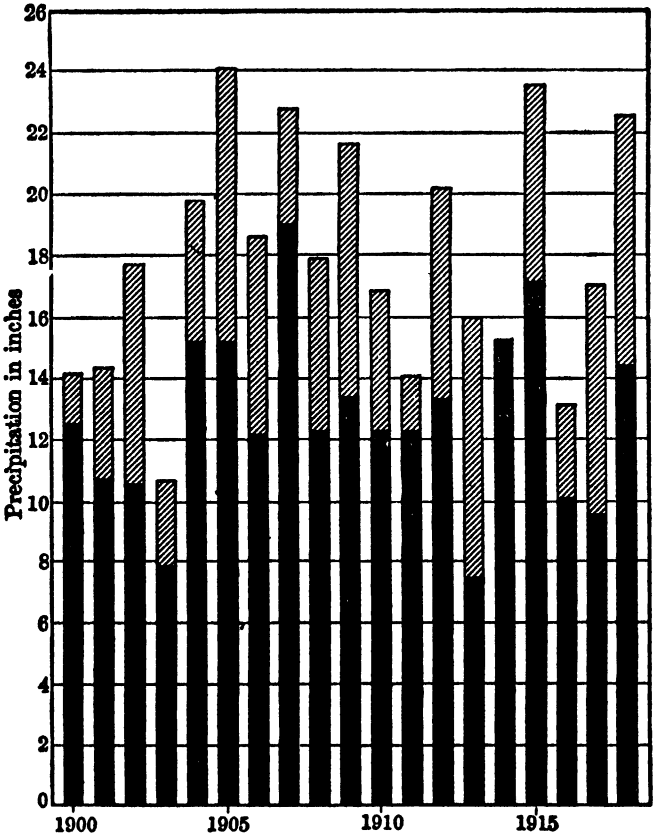


FIG. 17.—Graph of total and seasonal rainfall at Akron, Colorado.

Jones (1916:4), and McMurdo (1916:4). The graph of Williston rainfall (fig. 15) shows five 2-year and two 3-year cycles since 1900, while the record since 1885 shows an almost complete series of 2-year cycles. The Cheyenne graph shows a preponderance of 3-year cycles, and with the exception of a single year (1908), there is a perfect succession of 2-year and 3-year cycles. At Akron the first two cycles are 2-year and the last three are 3-year. At Amarillo the cycles are much less distinct, but the 3-year cycle is fairly well marked, especially in the seasonal rainfall. A comparison of the respective graphs will disclose the regional rainfall balance during a particular year. The year 1905 was excessively wet at Amarillo, Akron, and Cheyenne, but was very dry at Williston, 1906 being the wet year. Likewise, a slightly less wet year (1915) was excessively wet at Amarillo and Akron, only a little above the normal at Cheyenne, and slightly below normal at Williston, the

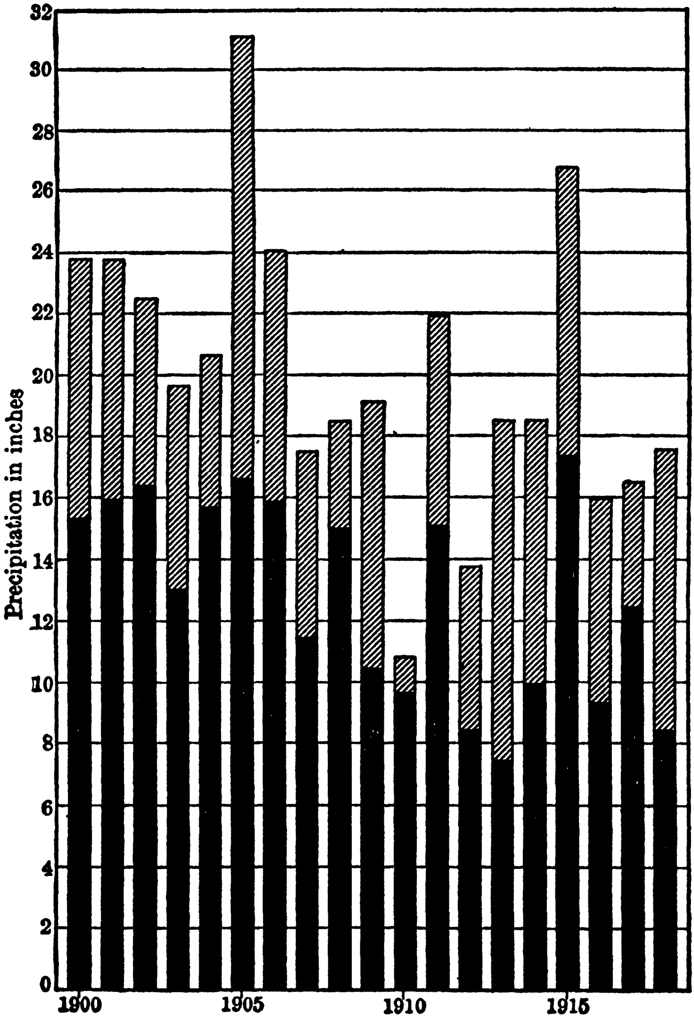


FIG. 18.—Graph of total and seasonal rainfall at Amarillo, Texas.

excess falling the next year again. The year 1911 was the driest of the record at Akron and Cheyenne, while it was nearly normal at Williston and above normal at Amarillo, 1910 being the driest year at both these places. The year 1914 was dry at Akron and Cheyenne, nearly normal at Amarillo, and above normal at Williston. The regional variations in seasonal rainfall, both absolute and relative, are even more marked. In 1915, the year of greatest seasonal rainfall at Amarillo and Akron, they received 18 inches from April to August inclusive, Cheyenne 10 inches, and Williston 6 inches. The seasonal rainfall was respectively 66, 55, and 50 per cent of the annual for the year. The year of greatest relative seasonal rainfall was that of 1910 at Amarillo, when 90 per cent of the annual rainfall came during the growing season. The corresponding values for Akron, Cheyenne, and Williston were 73, 50, and 70 per cent respectively (figs. 15-18).

Anticipation of cycles.—Crop production makes much greater demands as to the forecasting of rainfall than either grazing or forestry. These deal primarily with perennials, and in the case of trees in particular the dependence upon the summer rainfall is much less marked. As a consequence, a knowledge of the probable occurrence of the wet and dry phases of the 22-year and 11-year cycles or of the approximate total rainfall for any year is of much value. With annual crops the case is very different. While there is a general relation between annual and seasonal rainfall, the latter may vary between 50 and 90 per cent of the annual, as at Amarillo. Moreover, the distribution and timeliness of the seasonal rainfall are even more critical (Ball and Rothgeb, 1918: 24, 6). It must be frankly admitted that at present there are almost no clues to either distribution or timeliness, but this is due largely to the fact that their correlations have received almost no intensive study. It seems not improbable that the same basic processes of action and reaction and of compensating balance apply during the year and season as during cycles, and that they must be considered with reference to spatial variations as well. It is probable that the most important clue to the annual and seasonal rainfall of a particular year lies in the excess-deficit cycle of 2 to 3 years, which Arctowski has noted in crops and Douglass in trees. The assumption that a cycle of similar character may apply to the months receives striking confirmation from the studies of Douglas (1919) on the relation of weather to business. The general correlations of climate with production and prices and the existence of economic cycles have been dealt with by Moore (1914, 1917). All of these represent independent investigations and can hardly fail to strengthen the view that both long-period and short-period cycles occur in crop production (figs. 19 and 20).

In the endeavor to definitize climatic and production cycles and to discover a working basis for their prediction, investigations are under way to determine the climates and subclimates of the West on a plant basis. It is hoped to ascertain the response to the 22-year, 11-year, and 2 to 3 year cycles in terms of tree growth, grass yield, and crop production for different regions, suggested by the type or amount of rainfall. It is expected that the general correlations between rainfall and production will serve to mark the climates proper, but that the latter will show a series of subdivisions leading to restricted localities as the units upon which the practical anticipation of rainfall must be based. In any event, it seems clear that the attack upon this

vital problem from both the intensive and extensive approach will disclose new facts and leads and will bring nearer the actual utilization of cycle predictions in crop production.

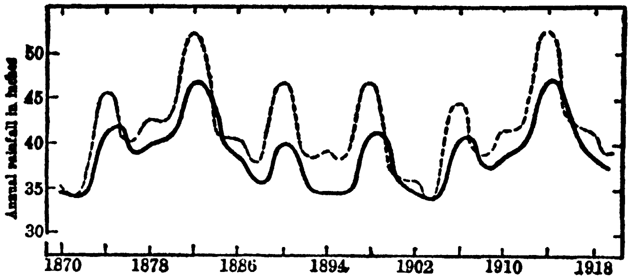


FIG. 19.—Cycles of rainfall in the Ohio valley, ..., in Illinois, ——. After Moore.

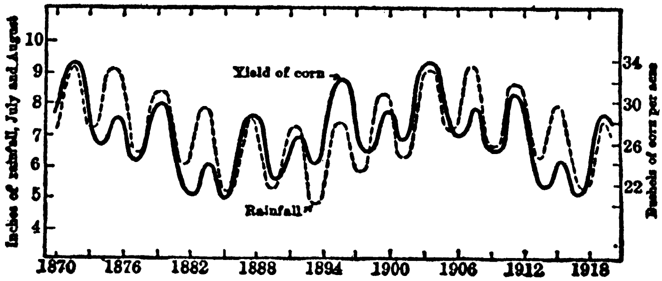


FIG. 20.—Cycles in the yield of corn and in the rainfall of its critical period of growth. After Moore.

XV. GRAZING INDICATORS.

Kinds of grazing.—Grazing practice depends primarily upon the kind of stock, the nature of the vegetation, the season, and the degree of control of the range. It varies more or less with all of these, but often to a much smaller degree than the best management would require. The four kinds of stock usually handled, namely, cattle, horses, sheep, and goats, not only have more or less definite preferences as to the type of grazing, but their effect upon the latter is also markedly different. In addition, they differ much in herding management and its relation to carrying capacity. With respect to grazing type, cattle and horses prefer grasses, sheep prefer herbs and weeds, and goats prefer shrubs or "browse." While this distinction is far from absolute, it marks a fundamental preference upon which the best practice must be built. It is the basis of mixed grazing, in which cattle and sheep, or cattle, sheep, and goats, are grazed upon a range at the same time. Mixed grazing is especially indicated in the ecotone between the chaparral, desert scrub or sagebrush and grassland, but it is desirable in practically all associations except such pure grass types as the short-grass plains. The maintenance of the proper carrying capacity in any type depends upon a knowledge of the difference in habits of stock with respect to the closeness and thoroughness with which each grazes, the amount of trampling, trailing, etc.

The handling of both herd and range depends in the first degree upon the season during which grazing is possible or desirable. The time and duration of the grazing season are determined partly by the behavior of the natural cover and partly by climatic conditions, chiefly the cold and snowfall of winter. In the North, where the winters are long and severe, summer constitutes the sole grazing season and both feeding and protection are either highly desirable or absolutely necessary for approximately half of the year. In the central portion of the West the summer grazing lies largely in the mountains and the winter grazing in the plains and valleys, permitting the regular movement of stock from one to the other. This is determined chiefly by the period during which the high summer ranges are accessible, but in some cases by the furnishing of water through winter snows, as in the Red Desert of Wyoming. In the Southwest the mild climate of winter permits handling stock on the range throughout the year, and the only limitations to this method are set by lack of water or feed. However, while year-long grazing has been the rule for many years throughout this region, the frequent recurrence of drought has shown the necessity of complete utilization of the high summer ranges, and the desirability of more or less winter feeding. This is the one region in which there is a distinct winter forage composed of annual herbs, with the interesting consequence that summer and winter grazing are normally possible on the same area.

The nature and degree of control of the range have a definite bearing upon grazing. This is largely concerned with the carrying capacity, but in cases of overgrazing it is the latter which determines the sufficiency of summer or winter range and the kind of grazing possible upon it. It is a well-known fact that the open range of the West has greatly deteriorated under existing con-

ditions, in which the only title the stockman can acquire inheres in keeping his particular range so constantly overgrazed that no one else will be tempted to use it. It is evident that a proper carrying capacity can be redeveloped and maintained on such areas only through the assurance of control. This has been secured in Texas by the private ownership of grazing lands, while in the case of the summer ranges of the national forests it has been provided by a system of grazing allotments. For the immense acreage still in the public domain, adequate control can best be obtained by a proper leasing system, as is shown in a later section. After the individual stockman has secured the exclusive use of his range under proper restrictions as to overgrazing, it is of secondary importance whether control is maintained by herding, drift fences, or complete inclosure. As will be seen, however, the latter method alone permits the maximum conservation and utilization of the natural forage crop.

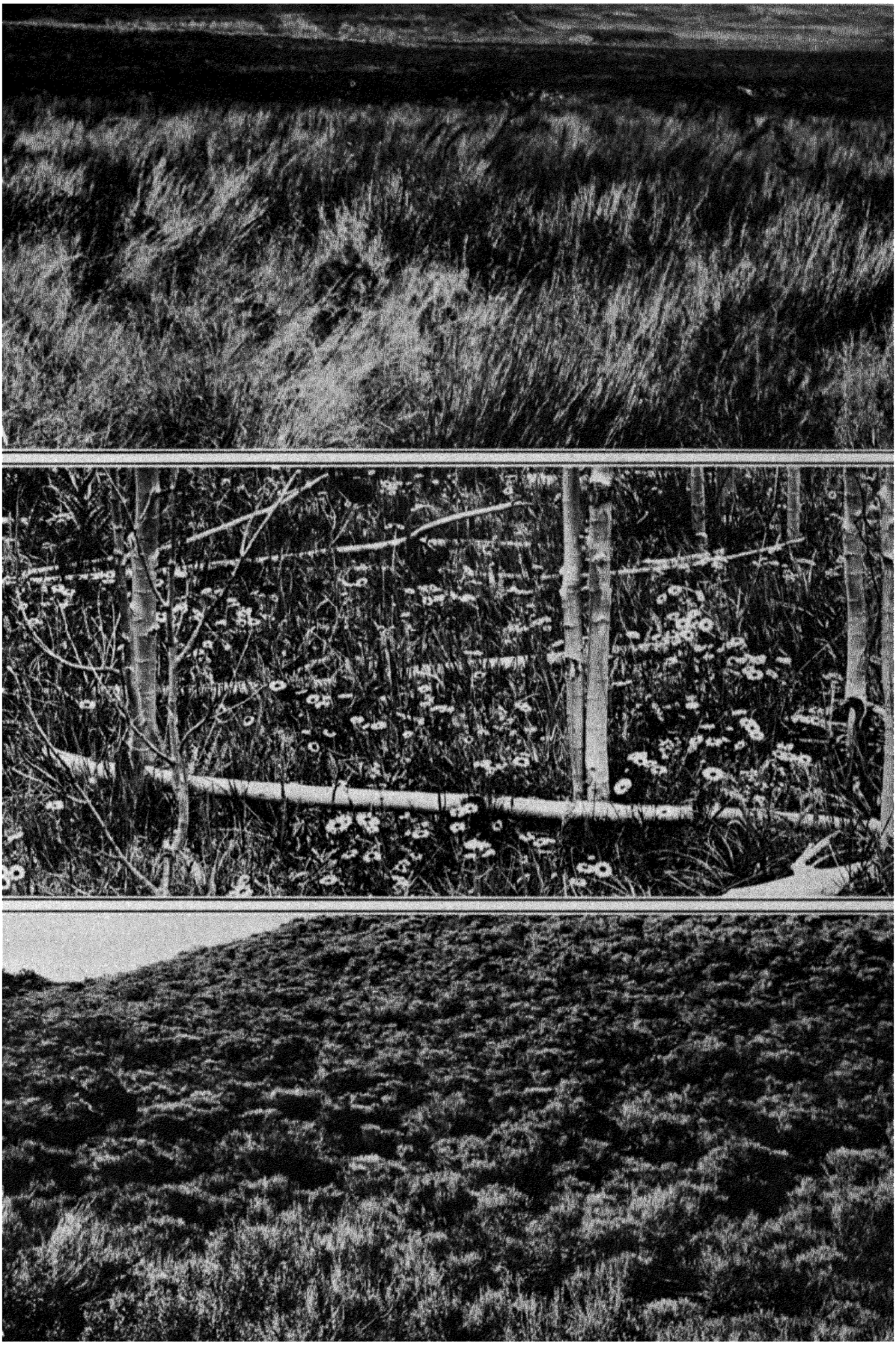
GRAZING TYPES.

Kinds of grazing indicators.—The simplest and most obvious indication of a plant community is that which denotes the possibility of grazing. To-day this is so axiomatic for grassland and scrub associations as to be entirely taken for granted. This has not always been the case, however (Wilcox, 1911: 35), and even at present there are forest and seral communities in which grazing indicators furnish a decisive test of the desirability of utilizing them. In the first instance, grazing types may be grouped as grass, weed, browse, and forest, and used to indicate the kind of grazing. The general principle in effect here is that a uniform community of grass, weed, or browse indicates cattle, sheep, or goats, respectively, while a prairie or a grass-scrub mictium or savannah denotes mixed grazing of two or three kinds of animals. The most striking and useful indicators are those which have to do with carrying capacity and overgrazing. These make it not only possible to measure the amount of carrying capacity and the degree of overgrazing, but they also reveal any failure to secure proper utilization. In addition, they serve to indicate the annual variations in forage production and to permit the correlation of these with the wet and dry phases of the climatic cycle. They likewise disclose the effect of local disturbances, especially those due to rodents, and they furnish a means of tracing the effects of eradication. As a consequence, they afford a complete basis for maintaining a proper balance between the utilization and conservation of the range and are of the greatest service in developing and applying an adequate system of range or ranch management.

The grouping of indicator communities as grass, weed, browse, and forest (Jardine, 1911) is one of both general and practical value. It permits subdivision into as many minor communities as desirable (Shantz and Aldous, 1917), and the chief consideration is to correlate these as naturally and effectively as possible. For this, no system approaches in value that of the developmental relationship as exhibited in the various climaxes and their successional stages. The climaxes indicated in Chapter IX illustrate the three main types, grass, scrub, and forest, while the seral communities and subdominants frequently exemplify the weed type as well. With reference to the grazing value, however, forest and woodland are to be classified on the basis of their undergrowth as grass, weed, or browse. It makes little difference practically whether grazing types are first grouped on the basis of their nature,

as grass, browse, etc., or on that of development, as climax and seral. The best system will necessarily employ both, but the vast extent of the climaxes and their obvious dependence upon the vegetation-form suggests them as the preferred basis. This has the further advantage of making the practical and the ecological system the same and of avoiding the confusion which exists in forestry, where the practical types and ecological units are often wholly different. The developmental method is also desirable in that it furnishes a uniform method of dealing with finer and finer divisions upon the basis of climate, soil, and region, as well as upon that of ecology and floristic. As all of these enter into practice sooner or later, it seems clear that the best treatment of grazing indicators is that which relates them to the proper formation and association. In consequence, the following discussion deals first with climax communities as indicators as much the most important, and then with the more localized seral communities. In addition, some account is taken of artificial communities due to planting or other modification, since it is assumed that these will play an increasingly larger part in the grazing industry of the future (plate 33).

Significance of climax types.—The value of the climax community as an indicator rests primarily upon the characteristic life-form. This is clearly seen in the three types, grass, weeds, and browse, but in the case of forest it depends upon the life-forms of the layers and seral stages. Climax formations are far more extensive than the developmental stages which occur here and there in them. Moreover, such stages are constantly moving toward the climax condition, slowly in the case of priseres and rapidly in the case of subseres. The climax communities are extensive and permanent, the seral ones local and temporary as a rule. As a consequence, the grazing practice of large regions must be based upon the indications of the climax formation or its subdivisions, while in a particular locality the importance of certain seral communities may demand some modification in practice. Apart from the vegetation-form as shown in grass, herb, shrub, or tree, the habitat-form and growth-form of the dominants must also be taken into account. Communities of sod-forming grasses indicate different values and treatment than those of bunch-grasses, while there is a striking difference between the associations of tall-grasses and of short-grasses. Climax communities of dominant herbs do not exist, but prairie and alpine meadow often contain so many mixed societies that the grazing value depends largely upon them. The indications of shrubs vary with the deciduous or evergreen nature of the leaf, succulence, form, ability to make root-sprouts, fruit, etc. The dominant trees of climax forest enter the question of grazing very little if at all, and the grazing type of each forest is determined by the greater abundance of grass, weeds, or browse. Finally, the grazing value of a community, and hence its indicator meaning, depend greatly upon whether it is pure or mixed. This is partly a matter of the relative value of the dominants as forage, and partly of the degree to which each is grazed and of its ability to grow and reproduce under the existing conditions. Mixed communities greatly predominate, and their utilization is determined to a large degree by the kind of mixture. They may consist almost wholly of dominants of the same vegetation-form, such as the short-grasses of the *Bulbilis-Bouteloua* plains, or they may contain shrubs and grasses, as in savannah. In addition, grassland which exhibits a marked



A. Grass type, *Andropogon-Bulbilis-Bouteloua,* Smoky Hill River, Hays, Kansas.
B. Weed type, *Erigeron, Geranium,* etc., in aspen forest, Pike's Peak, Colorado.
C. Browse type, *Artemisia tridentata,* Beulah, Oregon.

development of societies is essentially a mixed community with respect to grazing, since it permits selection by cattle or sheep, or mixed grazing by both.

Formations as indicators.—As has just been seen, the grazing value of a climax formation is determined primarily by the vegetation-form, though other factors enter locally to modify it more or less. The grassland climax is by far the most important of all, and there is little doubt that its development and extension have controlled the evolution of grazing animals in the past. The fact that the word *graze* is formed directly from *grass* proves that grassland has long been the primary grazing type, and that all others are secondary, resulting from the natural extension of grazing into scrub and forest. The alpine meadow ranks next to prairie and plain in primary grazing value, though the short season finds expression in the low growth-form as well as in the short period for grazing. The savannah marks the transition from primary grazing land, *i. e.*, grassland, to scrub. In spite of the unique importance of the latter for mixed grazing, its actual grazing value is secondary, as is indicated by the application of the word *browse* to it. Of the scrub climaxes, the chaparral usually stands first in importance, the sagebrush next, and the desert scrub last, though this varies greatly with the grouping of the various dominants. Of the forest formations, montane forest has the greater value, due largely to the open grassy nature of the yellow pine consociation. The woodland resembles the latter more or less and often ranks next to it in amount of grazing. The subalpine forest varies greatly in importance. The grazing value of its meadows, natural parks, and aspen areas is high, but the climax forest is usually too dense and closed to permit the growth of a uniform ground cover. This is even truer of the luxuriant Coast forest, in spite of the fact that the latter often exhibits a dense tangle of shrubbery.

Associations as indicators.—The indicator significance of an association is essentially that of the formation to which it belongs. As a subdivision, it represents a closer response to regional conditions, and the various associations of a climax permit the recognition of more or less different grazing values. This is characteristically true of the grassland and alpine meadow formations. It holds to a somewhat smaller degree for the scrub and is least evident for the forest climaxes, in which the number and extent of seral communities are more significant for grazing than the climax areas themselves.

In determining the relative grazing value of the associations of the grassland climax, this is found to depend upon density, height, and mixture. Upon this basis, the subclimax prairies are perhaps the most valuable, though the true prairies are nearly as valuable, and in some cases even more so. The mixed prairies come next, and are followed by the short-grass plains. The bunch-grass prairies at their best may equal the latter, but generally the stand is too open. While the desert plains are of the same character as the short-grass association, the bunch habit is more pronounced and the total production usually less. Quite apart from the question of yield, however, is that of time of development and ability to cure on the ground. From this standpoint, the mixed prairie of tall *Stipa* or *Agropyrum*, and short *Bulbilis*, *Bouteloua*, or *Carex*, or the transition area of *Andropogon* and short-grasses has a distinct advantage. The tall-grasses either develop earlier or grow with such rapidity as to furnish the bulk of spring and summer feed, while the

short-grasses become cured in late summer to furnish feed for fall and winter. Finally, it must be recognized that the tall-grass associations are agricultural indicators as well, and that economic considerations give them greater significance in this rôle. Our knowledge of the Sierran alpine meadow is too small to enable us to draw an accurate comparison with the Petran association. They are so nearly alike in the growth-form and genera of the dominants and in the number and luxuriance of the societies that they exhibit no clear difference in yield per unit area. In spite of this, the Petran association is actually very much more important, for it covers an area many times greater, is more coherent, and for the most part covered by snow to a less degree and for a shorter period.

The grazing value of the chaparral associations depends largely upon the presence of oak, which is usually the most important of the dominants for browse. For this reason, the Petran chaparral is usually more important than the Coastal, though its value decreases greatly with the dropping out of the oak to the northward, just as it increases to the southeast with a larger number of species of *Quercus*. In the sagebrush formation, the Basin association is all-important, the Coastal community being of relatively small extent and containing but one or two dominants of value. The differences between the associations of the desert scrub are not so clear-cut, but the advantage lies in general with the western community, owing largely to the much greater number of succulents. The three associations of the woodland exhibit a thin ground cover of grass and shrubs, resulting from the combined effect of dryness and shade. They produce savannah where they are in contact with grassland or scrub, and in such cases possess more or less of the grazing value of the latter. The presence of oak gives woodland some value as browse, and in this respect the oak-cedar community stands first and the pine-oak next. The montane associations differ strikingly in ground cover, the Petran having the herbaceous layers best developed, and the Sierran, the shrub layer or so-called subclimax chaparral. The former has usually the greater importance for grazing, since many of the shrubs of the chaparral are unpalatable. The comparative value of the associations of the subalpine forest is less certain, but on the whole the Petran has the advantage, especially when the seral grasslands are taken into account.

Consociations as indicators.—The value of the consociation as an indicator is determined primarily by the life-form. Grassland derives its unique importance for grazing from the grass dominants, while the value of scrub dominants is much lower and more variable, and that of forest consociations almost wholly dependent upon the undergrowth. In the grassland the chief value lies in the consociation, with the scrub in the consociation and its societies, and in the forest it lies in the shrub and herb societies alone. Moreover, grass consociations are true grazing types, scrub are primarily browse types, and forest and woodland are grazing or browse, depending upon the relative abundance of herbs and shrubs. Consociations may be pure or mixed, and the indicator meaning naturally varies accordingly. While mixed communities are the rule, pure consociations are sufficiently frequent to permit the determination of carrying capacity, response to overgrazing, and other features which make up the total grazing value. In the case of mixed communities the analysis is based upon the normal response of each pure consociation,

modified by their varying relations to the grazing animals and their competitive reactions upon each other. In dealing with the actual grazing types of a particular region, pure consociations play an even smaller part on account of their relatively small extent. While they are very helpful in ecological analysis, they are of little importance in practical management.

Local grazing types.—While the main grazing types, such as the formation and association, indicate the comparative value of great regions, as well as the groupings possible in any one, it is the local groupings which determine the carrying capacity of a particular ranch and the proper system of management to be employed upon it. For this reason, they may well be termed practical grazing types. In areas relatively uniform, a single grazing type composed of the two or three major dominants of the association may cover a wide extent. This is the case with *Stipa* and *Bouteloua* in North Dakota and Montana, *Bulbilis, Agropyrum,* and *Bouteloua* in the region of the Black Hills, and *Bulbilis* and *Bouteloua* in Oklahoma and Texas. As a rule, however, changes in topography or soil or in the number and grouping of the subdominants bring about important changes every few miles, and very frequently adjoining sections will be found to have a different grouping or an effective difference in relative abundance. Hence, it is clear that the local community must determine the careful classification of the land section by section, especially with reference to carrying capacity, as well as the method of management. For example, while all the climax groupings in the mixed prairie resemble each other in structure and treatment much more than they do groupings of the true prairie or short-grass plains, they show decisive differences among themselves. The carrying capacity and relation to overgrazing of the *Stipa-Bouteloua* community differ from that of *Agropyrum-Bulbilis,* and of both of these from that of *Bulbilis-Agropyrum-Bouteloua.* The marked development of societies reduces the abundance of the dominant grasses, and at the same time affects the carrying capacity. The relation between the two effects depends upon the degree to which the subdominants are grazed, but as a rule they are less palatable than the grasses. Over regions of rolling topography, such as prairies and sandhills, the climax groupings are regularly interrupted by valley and ridge communities which are successional in nature. These are of relatively small extent and may frequently occur with the climax grouping on a ranch of a section or less in extent. In the case of the more level plains, the seral communities are confined to stream valleys and breaks and cover much larger areas. They often serve to mark the distinction between valley and upland ranches. They are not confined to one association, but such a grouping as that of the *Andropogons* may be found repeatedly from the true and mixed prairies through the short-grass and desert plains.

The number of such groupings is legion, and the most important occur again and again in the region where they are characteristic. They have been found in sequence over many thousands of miles in the West. They are of the first importance in determining local variations in grazing value and are regarded as the basic indicators to be used in the range survey discussed later. As already indicated, the major indication of the grouping must always be interpreted in connection with the minor indication of the societies

short-grasses become cured in late summer to furnish feed for fall and winter. Finally, it must be recognized that the tall-grass associations are agricultural indicators as well, and that economic considerations give them greater significance in this rôle. Our knowledge of the Sierran alpine meadow is too small to enable us to draw an accurate comparison with the Petran association. They are so nearly alike in the growth-form and genera of the dominants and in the number and luxuriance of the societies that they exhibit no clear difference in yield per unit area. In spite of this, the Petran association is actually very much more important, for it covers an area many times greater, is more coherent, and for the most part covered by snow to a less degree and for a shorter period.

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Consociations as indicators.—The value of the consociation as an indicator is determined primarily by the life-form. Grassland derives its unique importance for grazing from the grass dominants, while the value of scrub dominants is much lower and more variable, and that of forest consociations almost wholly dependent upon the undergrowth. In the grassland the chief value lies in the consociation, with the scrub in the consociation and its societies, and in the forest it lies in the shrub and herb societies alone. Moreover, grass consociations are true grazing types, scrub are primarily browse types, and forest and woodland are grazing or browse, depending upon the relative abundance of herbs and shrubs. Consociations may be pure or mixed, and the indicator meaning naturally varies accordingly. While mixed communities are the rule, pure consociations are sufficiently frequent to permit the determination of carrying capacity, response to overgrazing, and other features which make up the total grazing value. In the case of mixed communities the analysis is based upon the normal response of each pure consociation,

modified by their varying relations to the grazing animals and their competitive reactions upon each other. In dealing with the actual grazing types of a particular region, pure consociations play an even smaller part on account of their relatively small extent. While they are very helpful in ecological analysis, they are of little importance in practical management.

Local grazing types.—While the main grazing types, such as the formation and association, indicate the comparative value of great regions, as well as the groupings possible in any one, it is the local groupings which determine the carrying capacity of a particular ranch and the proper system of management to be employed upon it. For this reason, they may well be termed practical grazing types. In areas relatively uniform, a single grazing type composed of the two or three major dominants of the association may cover a wide extent. This is the case with *Stipa* and *Bouteloua* in North Dakota and Montana, *Bulbilis, Agropyrum,* and *Bouteloua* in the region of the Black Hills, and *Bulbilis* and *Bouteloua* in Oklahoma and Texas. As a rule, however, changes in topography or soil or in the number and grouping of the subdominants bring about important changes every few miles, and very frequently adjoining sections will be found to have a different grouping or an effective difference in relative abundance. Hence, it is clear that the local community must determine the careful classification of the land section by section, especially with reference to carrying capacity, as well as the method of management. For example, while all the climax groupings in the mixed prairie resemble each other in structure and treatment much more than they do groupings of the true prairie or short-grass plains, they show decisive differences among themselves. The carrying capacity and relation to overgrazing of the *Stipa-Bouteloua* community differ from that of *Agropyrum-Bulbilis,* and of both of these from that of *Bulbilis-Agropyrum-Bouteloua.* The marked development of societies reduces the abundance of the dominant grasses, and at the same time affects the carrying capacity. The relation between the two effects depends upon the degree to which the subdominants are grazed, but as a rule they are less palatable than the grasses. Over regions of rolling topography, such as prairies and sandhills, the climax groupings are regularly interrupted by valley and ridge communities which are successional in nature. These are of relatively small extent and may frequently occur with the climax grouping on a ranch of a section or less in extent. In the case of the more level plains, the seral communities are confined to stream valleys and breaks and cover much larger areas. They often serve to mark the distinction between valley and upland ranches. They are not confined to one association, but such a grouping as that of the *Andropogons* may be found repeatedly from the true and mixed prairies through the short-grass and desert plains.

The number of such groupings is legion, and the most important occur again and again in the region where they are characteristic. They have been found in sequence over many thousands of miles in the West. They are of the first importance in determining local variations in grazing value and are regarded as the basic indicators to be used in the range survey discussed later. As already indicated, the major indication of the grouping must always be interpreted in connection with the minor indication of the societies

present. In its application to grazing at least, the grouping is so important that the need of a more distinctive term is clearly felt. In so far as grazing is concerned, the term grazing type might well serve the purpose, though formations and associations, as well as seral communities, are also grazing types. The grouping of consociations within the association is typical of all climaxes, however, and seems to warrant a special term for those who need a complete and detailed analysis of vegetation. After an extended consideration of the possibilities, it has seemed desirable to definitize the term *facies* for seral groupings and to make a new word, *faciation*, for climax groupings. These are derived from the same root, *fac*, shine, and possess the same basic meaning, namely, appearance, aspect, or form. The two terms conform to the mutual relation seen in associes and association, consocies and consociation.

Savannah as an indicator.—Throughout the present treatment, the word savannah is used for the community which characterizes the ecotone between two climax formations. In its most typical expression, it consists of grasses and low trees or tall shrubs, and occurs in the hot, dry regions of the Southwest. Other communities are so similar that it is impossible to exclude them, and hence open pine forest and woodland with a grass cover are also called savannah. Closely related to these are the so-called natural parks of the Rocky Mountains in which seral grassland is surrounded and more or less invaded by trees. Such parks occur in both the montane and subalpine zones. When the ecotone lies between forest or woodland and scrub, the general ecological relations are similar to those of savannah, but the grassland is replaced by sagebrush, chaparral, or desert scrub. The trees stand more or less scattered in the scrub, and the indications of the community are primarily those of the latter. The failure to recognize this similarity to savannah has led to confusion with reference to the distinctness of the scrub climaxes in rough regions where they are interspersed with trees. Savannah has been so generally linked with the presence of grasses that it seems unwise perhaps to broaden its meaning to include areas of scrub with taller trees, and consequently the word park has been used for the latter. Thus, a sagebrush savannah is one in which sagebrush is scattered through grassland, while a sagebrush park is a community in which sagebrush is surrounded and more or less invaded by trees or tall shrubs.

In their typical form, both savannah and park are controlled by the grasses or scrub, and the trees are more or less incidental. The transition to forest or woodland is usually gradual, and it is impossible to draw a sharp line between the two. However, it is a simple matter to distinguish the general areas from each other. As long as the trees or shrubs are far enough apart so that their shadows do nót touch, the grassland or scrub remains in control. When they are sufficiently close to have their shadows overlapping during most of the day, the grass or scrub dies out for lack of sun, or persists only in small groups of much modified individuals. Tree and scrub savannah often cover extensive areas to which they give the appearance of open woodland, but the true nature of the community is indicated by the continuous carpet of grass, which serves as the indicator. Sagebrush and chaparral parks are usually more local, and they quickly pass into woodland on the one hand and scrub on the other. They recur constantly, owing to the relatively small

difference in requirements between shrubs and small trees. Savannah proper is probably due to the effect of climatic cycles and is thought to serve as an indicator of the wet phase of the cycle. The control of the grasses is so complete that the additional water-content necessary for the germination and establishment of the trees or shrubs is present only during the maximum of the wet phase, often only a single year. Once established, and with their roots at greater depths than those of the grasses, the trees or shrubs persist indefinitely. During succeeding wet phases they tend to increase in number, while in critical drought periods the number may be reduced, as is regularly the case where fires are frequent. Counts of the annual rings of a number of shrubs in different savannah areas confirm the view that ecesis is normally confined to wet phases of the climatic cycle.

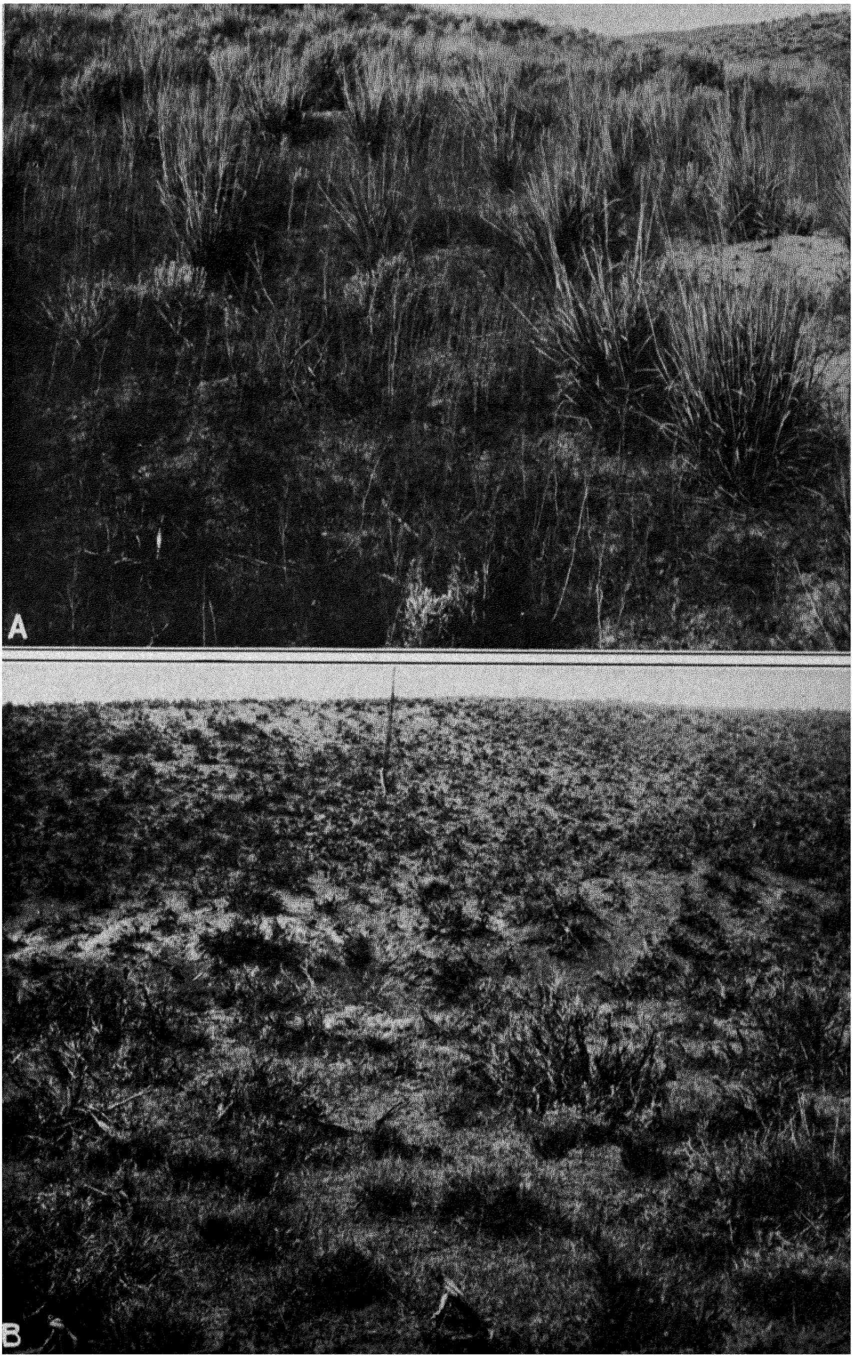
The indicator significance of savannah or park naturally depends upon the kind and the region, as well as upon the dominants. The best examples of tree savannah are to be found along the line of contact of forest or woodland with grassland. Oak savannah is the most common, occurring typically in central Texas, in Arizona, New Mexico, and Mexico, and in California and Lower California. Savannah in which yellow pine is the tree is frequent along the lower edge of the montane forest, where it extends out upon plateaus or plains. It is well-developed in northern Arizona and New Mexico, but is most extensive on the low ranges and high plains east of the central Rockies and around the Black Hills. Both piñon and cedar form savannah, but the latter is much more frequent and extensive. Typical scrub savannah is largely confined to the Southwest, ranging from Texas through southern New Mexico and Arizona, and northern Mexico. Its most characteristic shrub is mesquite, *Prosopis juliflora,* but *Yucca, Acacia, Ephedra,* and other dominants of the desert scrub occur frequently. Owing to its habit of growing in clumps or groups, chaparral tends to form grassy parks rather than typical savannah, especially along the edge of the Petran association. Sagebrush extends into several of the grassland associations to form what is essentially sagebrush savannah, though its low stature tends to obscure the exact relation. This is especially true where it meets the tall-grasses, as in Wyoming and Oregon, but the savannah nature is obvious where tall sagebrush is scattered through short-grass, as in southeastern Utah.

Parks differ from savannah chiefly in that the two communities concerned mix by alternating groups or areas rather than by scattered individuals. Excellent examples of grass parks occur in the subalpine forests of Colorado, where spruce and balsam inclose extensive meadows of *Festuca,* dotted with groups of young conifers or aspens. Somewhat similar parks occur at timberline, where the forest breaks into groups which extend well up into the alpine meadows. Sagebrush parks occur most commonly in the lower subclimax portion of the woodland zone, while sagebrush areas dotted with groups of lodgepole pine or aspen are frequent on the western slope of the Rocky Mountains in Colorado and Wyoming. Chaparral parks are best developed in California, especially in the case of subclimax chaparral in the pine forest and where the climax type meets the pine-oak woodland. In the Rocky Mountain region they occur chiefly as scrub openings in the piñon-cedar or oak-cedar woodland.

Savannah and park are alike as indicators in that they denote a transition

from one community to another. They differ for the most part in that savannah is an indicator of climate, and park usually of local or edaphic conditions. Savannah has to do with the relations of two contiguous climaxes, and park with that of a subclimax to its climax. The former is a permanent condition, varying more or less under the influence of the wet and dry phases of climatic cycles, while the latter is usually a temporary community, occupying its proper place in prisere or subsere, and passing ultimately into the climax. Hence, the indicator values of different types of parks are dealt with in the next section, while those of savannah are considered here. True savannah has value as an indicator of climate as well as of practice. It not only indicates a transition between the climates of the respective climaxes, but also serves to record the course of the climatic cycle. The amount to which it increases its area and density under the same conditions is a measure of the effect of the wet phase, and the dying-out of individuals, of the dry phase. Such measurements are possible only under control, however, owing to the almost universal disturbance of fire or overgrazing.

Kinds of savannah.—With reference to practice, savannah indicates the general possibility of agriculture. For the most part, this is of the dry-farming type, though in central Texas it indicates humid or subhumid farming, and in California farming by means of drought-evasion. With respect to grazing, the indications of savannah depend primarily upon the grass dominants. In fact, the indicator value of savannah is essentially that of the grassland community, unless the trees or shrubs are sufficiently close to reduce materially the amount of grass. When the shrubs themselves have distinct value as browse, the carrying capacity becomes greater than that of the grassland alone, and mixed grazing is also favored. The yellow pine savannah of the Black Hills and eastern Rocky Mountain region occurs in the mixed prairie, while in the Southwest it lies in the short-grass associes. In both cases, the grazing value of the grassland is practically unchanged, except for some reduction in cover just beneath the trees. Pine savannah also occurs along the upper edge of the bunch-grass prairie, but it is rarely extensive here. Cedar savannah is found chiefly in the short-grass community, but is frequent also in the desert plains and mixed prairies. Where the cedar is low, it materially reduces the total carrying capacity, though this is often offset by the presence of browse shrubs. Mesquite savannah lies typically in the desert plains, though the mesquite itself extends northward into the short-grass associes of the Staked Plains. The shrubs have little effect upon the amount of grass, and they change the indications of the community only to the extent that they are valuable for browse. Toward the lower edge of the savannah the shrubs become denser as they pass into the desert scrub, and the grassland rapidly decreases to the point of disappearance. Oak savannah may be of the tree or shrub type. The latter is most typical on the plateaus and mountain ranges of southwestern Texas, New Mexico, Arizona, and Mexico, where it is formed chiefly by live-oaks. It lies in the desert plains grassland, or in the *Andropogon* zone just above. The grazing value due to the grasses is greatly increased by the abundant browse, and such savannah may well be regarded as one of the best of all grazing types, owing to the assurance it gives against drought in connection with mixed grazing. Tree savannah consisting of oaks usually has little or no



A. *Elymus* and *Agropyrum* reappearing as a result of fire in sagebrush, Boise, Idaho.
B. Sagebrush dying out as a result of competition with *Agropyrum*, Craig, Colorado.

browse value, and its indication is essentially that of the grass community in which it is found, with some reduction caused by shading. In California, the original *Stipa* bunch-grass prairie has been almost wholly replaced by the wild-oats, *Avena fatua,* and the latter determines a relatively lower value for the community. The sagebrush savannah so characteristic of northeastern Wyoming lies in the edge of the mixed prairie, and the sagebrush is chiefly associated with *Stipa,* though *Agropyrum* and *Bouteloua* are also present to a large degree. The relative abundance of grass and sagebrush varies widely, and the indicator value of the mixture in accordance. Since the sagebrush is eaten to a much less degree during the summer, the carrying capacity is somewhat reduced, though this is partly compensated by its availability during the winter.

Savannah in relation to fire and grazing.—The general view in the Southwest is that mesquite and oak savannah are limited or destroyed by fire and that they have spread rapidly in recent years, since the annual burning has ceased (Cook, 1908). In the absence of definite measurements, many of the statements can be accepted only in part, though the general relation to fire seems evident enough. Tree savannah appears to be affected little by burning, except that this must have been a powerful factor in spreading the annual *Avena* in California at the expense of the perennial *Stipa.* The effect of fire upon scrub savannah depends upon a number of factors, chief among which are density and height of both shrubs and grasses, the ability of the shrubs to form root-sprouts, and the frequency of fires. It seems certain that annual fires in scrub savannah that is densely covered with tall-grasses would destroy the shrubs completely in a few years, no matter how great their ability to form root-sprouts. Less frequent burning of open savannah, in short-grass especially, would damage the shrubs much less and might well increase their control by promoting root-sprouting. Moreover, in the more xerophytic grasslands, frequent burning during dry seasons injures the grass and would tend to favor the shrubs in consequence (plate 34).

The general effect of grazing is to increase the shrubs at the expense of the grass. As has been seen, savannah owes its character to a dry climate in which the ecesis of shrubs is regarded as usually possible only during the wet phase of the cycle. This means that shrubs and grasses live constantly under keen competition for water, and that anything which reduces the amount of grass will be to the advantage of the shrubs. Since grasses and herbs are usually eaten to a much larger degree, intensive grazing, and especially overgrazing, will reduce their hold upon the soil and correspondingly improve conditions for the spread of shrubs. The seeds of the mesquite and other shrubs are widely scattered as a consequence of being eaten or through unintentional carriage, and the seedlings are more readily established in areas where the hold of the grasses has been weakened. The local spread of the scrub clumps is chiefly by means of root-sprouts and is promoted by light browsing, but restricted by heavy browsing. Thus, while savannah is primarily an indicator of climate, its secondary indication is one of grazing and absence of fires, upon which its practical utilization must be based. As suggested in a later section, this can be done readily only after quadrat measures have made clear the exact behavior of savannah under different methods of burning and grazing.

Significance of seral types.—While seral communities are temporary in comparison with climax ones, many of them persist for tens or even hundreds of years, and in actual practice may be regarded as permanent. The great majority of them result from disturbance, however, and last for a period of a few years, or at most for a decade or two, unless the disturbance is continuous or recurrent. In addition, they show rapid changes of population from year to year. Such communities are usually local and of small extent and have resulted from fire, overgrazing, or cultivation. They belong to secondary successions or subseres in contrast to the larger and more permanent communities which constitute stages in the primary succession or prisere. These distinctions apparently disappear in the case of great stretches which are kept more or less permanently in the lodgepole or aspen community as a consequence of repeated fires, or in the *Aristida* or *Gutierrezia* stage as a result of continued overgrazing. Even here, however, the differences in the kind and rate of development are of great practical value in determining the proper management. As a consequence, it is desirable to distinguish seral communities as indicators upon the basis of primary and secondary succession, and then to deal with the indicator value of the respective dominants. Each of these is known as a consocies when it is controlling, and corresponds with the consociation among climax types. Two or more consocies regularly occur together to constitute a particular stage or associes, while their subdominants are known as socies, which correspond with the societies of climax communities. A complete treatment of seral indicators is neither possible nor desirable at present, but the following account will serve to illustrate all the important types.

Prisere communities as indicators.—The four great types of primary succession are those which start in initial bare areas of water, rock, dune-sand, or saline lake or basin respectively. The initial communities and some of the medial ones may be used as negative indicators, denoting that conditions have not reached the point where they can support a plant cover of such density or quality as to furnish grazing. The later communities, and especially the subclimax one that immediately precedes the climax, form a more or less complete cover in which grasses or shrubs are usually in control. The density of the cover and the quality of the grazing increase more or less regularly from the medial stages to the climax, and the position of a particular community in the sere indicates its value in a general way.

The most important seral indicators of grazing are the later stages of the priseres in dunes and sandhills, in bad lands and in salt basins. These often cover many thousand square miles and frequently occur in agricultural regions, where the indicator distinction between grazing and farming land is especially important. In addition, there are the sedge and grass meadows which are stages of the hydrosere, and are often characteristic of mountain parks in the montane and subalpine zones. Grassland and scrub also develop in rock fields and on talus slopes where the formation of soil is not too slow. While such parks and gravel-slide areas often afford excellent grazing, they are usually both local and relatively small and serve chiefly to increase the grazing value of the forest areas in which they occur.

Of all the prisere communities, those of sandhills and dunes are probably the most widely distributed and most important. They have been found and

studied in each of the 16 Western States, where they may occur as sandhill regions of large extent, as river dunes or ocean dunes. The most extensive sandhill areas occur in Nebraska, Kansas, and Colorado, though they are scattered throughout the grassland climax from North Dakota to Texas and New Mexico. Such areas differ from dunes chiefly in extent and complexity, and in the fact that they are no longer connected with an active shore-line from which the sand is derived. They are essentially stable dunes with blowouts as characteristic features, and for the most part they exhibit subclimax communities. The succession in sandhills and dunes is practically identical for the same climax, but differs greatly between climaxes, especially in the later stages. The largest and most important sandhill region is that of central Nebraska, which covers an area of about 20,000 square miles. It has received much study during the past 30 years, and the ecological results have been summarized by Pool (1914) in a monograph on their vegetation. The typical community of the sandhills is the bunch-grass subclimax, consisting of *Andropogon hallii* and *A. scoparius*. The blow-sand condition, typical of blowouts especially, is indicated by *Redfieldia, Psoralea,* and *Petalostemon,* which have little or no grazing value. More stable conditions are denoted by *Muhlenbergia* and *Calamovilfa,* and these are correlated with increasing grazing value. The next stage is that of the *Andropogon* subclimax, which possesses a much higher value. By the entrance of *Stipa* and *Koeleria,* the bunchgrass subclimax passes into the true prairie, while in the western portion the invasion of *Bouteloua* and *Bulbilis* indicates the appearance of the short-grass subclimax, or of mixed prairie when *Stipa* and *Agropyrum* occur also. The hydrosere is a regular feature of the innumerable wet valleys and of the extensive lake region. The first community to indicate grazing is composed of rushes and sedges, and this changes slowly into the typical meadow associes of *Agropyrum, Andropogon, Elymus, Panicum,* and *Spartina,* which is essentially an extra-regional portion of the subclimax prairie. The grazing value of such a group of dominants is obvious, but in practice such meadows are used for hay, since the hills furnish ample summer grazing.

Like the sandhills, bad lands are found throughout the West. Massive bad-land complexes are most typical of the States which touch the Black Hills, but they are frequent also in practically all those along the Rocky Mountain axis, while outlying areas of much interest are found in Texas, Oregon, and California. The actual communities of the sere likewise differ with the climax. The two most important seres are the xerosere of the Tertiary bad lands in the Great Plains region of the grassland climax, and the halosere of the Great Basin sagebrush climax. The former possesses a number of herbaceous stages which have an increasing value for sheep-grazing as they become denser, but grazing proper is indicated only when *Agropyrum* becomes abundant. *Bouteloua* and sometimes *Bulbilis* also enter somewhat later to form mixed prairie, and the latter then becomes definitely constituted by the appearance of *Stipa.* The lower valleys are often controlled for a time by sagebrush, but this ultimately yields to the grasses. The juxtaposition of weed, grass, and sagebrush types indicates the value of bad land areas for mixed grazing, and suggests the importance of hastening the course of succession in them. The bad lands of the sagebrush climax are characterized in the initial stages by colonies of halophytic annuals, which have some grazing

value where they make a definite cover. The first stage of much importance is formed by the low perennial species of *Atriplex,* such as *A. nuttallii, A. corrugata,* and *A. pabularis.* These are followed by *Atriplex confertifolia* and *Grayia,* which furnish forage of much better quality and larger amount, and these are finally invaded by *Artemisia tridentata* to form the mixed or pure grazing type so characteristic of the Great Basin and its outlying regions. In the bad lands of the Painted Desert in northern Arizona, the general course of the sere is much the same, but the grasses replace *Atriplex.* The normal sequence in the subclimax stages is the replacement of *Sporobolus airoides* by *Hilaria jamesii,* and this by *Bouteloua,* often with *Muhlenbergia also.* The course of development in the halophytic bad lands is essentially a part of the widespread succession in saline basins, except that the latter often begins in water. Shantz (1916 : 233) has indicated the course of the succession in detail, and it must suffice to point out that the first important indicators of grazing are usually scrub dominants, *Sarcobatus* and *Atriplex.* Some of the playas of the Southwest are intensely saline, and show essentially the same communities, but the majority are secondary in nature and belong to the subsere.

Subsere communities as indicators.—Subseres are developed in secondary areas, such as are regularly produced by fire or cultivation. They occur also in other bare areas in which the disturbance is not sufficient to destroy the soil or to make extreme conditions for ecesis. They are a constant feature of overgrazing and a normal consequence of the presence and activity of man. They are usually local and of small extent, but in the case of fire they may occupy hundreds of square miles. The successional movement is normally rapid, but its progress may be slowed or stopped by the recurrence of the disturbing agency. When this is the case, the area concerned may be held more or less permanently in a subclimax or other seral stage. The most important and extensive subseral communities are those due to fire. The consequences of overgrazing often cover great stretches, but the actual communities change more or less, or they are much intrrupted. Those due to cultivation are usually confined to fields, though many of the dominants become extended to roadsides, and some even enter the natural vegetation. While they often have grazing value, it is incidental and temporary and their chief value lies in connection with utilization as supplementary forage crops, as already indicated for *Salsola, Helianthus, Melilotus,* and others.

Certain grasses, such as *Poa, Avena,* and *Bromus,* have become widespread dominants as a consequence of the combined action of two or more agencies. In the case of *Avena* and *Bromus,* the species concerned, *A. fatua, B. tectorum, B. rubens,* etc., are annuals which have replaced the native dominants as a general result of the combined effect of overgrazing and fire. As annual grasses, these should have a low grazing value, but this is much less true of *Avena* than *Bromus,* owing largely to the difference in size and habit. Even *Avena* is less valuable than the native perennial grasses which they usually replace, and this suggests the desirability of taking advantage of the principles of succession to restore the original community where it has not been completely destroyed. *Poa pratensis* as a perennial grass of meadows has practically the same ecological habits and grazing value as the prairie dominants which it replaces. Its rapid spread in the valleys and ravines of the

true prairies seems to have been the result of a certain amount of disturbance, but *Poa* is not a true seral consocies, such as the annual *Avena* and *Bromus*. Among other such consocies of importance are *Plantago patagonica*, *Portulaca oleracea*, *Boerhavia torreyana*, and *Polygonum aviculare*. These are all indicators of disturbance, particularly overgrazing, but in the green condition they also have more or less value as indicators of an available weed type. Other indicators of disturbance are represented by such plants as *Hilaria mutica*, *Scleropogon brevifolius*, *Franseria*, and *Bulbilis*. These occur in playas or "swags" which are subject to flooding and in which a thin annual layer of silt is often deposited as well. The first two are commonly associated, partly owing to the fact that the disturbance of the *Hilaria* consocies by trampling and overgrazing favors the spread of *Scleropogon*. Tobosa swags are typical seral areas in the desert scrub as well as in the zone of savannah which lies between this and the desert plains. In the latter particularly, *Hilaria* is a characteristic subclimax, in which *Scleropogan* is usually an indicator of grazing disturbance, frequently with a similar associate, *Sporobolus auriculatus*. *Hilaria* is an indicator of summer grazing, while the other two are rarely grazed except under drought conditions. The playas of the southern Great Plains are marked by a similar subsere, in which *Franseria* is the important early stage and *Bulbilis* the subclimax. Both of these are grazing indicators, though the value of the *Franseria* is relatively small.

Fire indicators and grazing.—The typical indicators of fire are trees and shrubs, and they may have a direct or indirect relation to grazing. The indicators may themselves be browsed, or they may be associated with layers of herbs or shrubs which furnish feed. Grasses and other herbs may indicate fire, but are usually associated with woody indicators or their relics. The most important "burn" communities are pine forest, aspen woodland, chaparral, and savannah. In addition, there are grass and sagebrush parks which also represent subseres initiated by fire. Savannah has already been considered, while the grazing value of grass parks is obvious. Sagebrush and chaparral are primarily browse types, though they contain a larger or smaller amount of grass or herbs as well. When young, aspen woodland furnishes a large amount of browse, but it is chiefly valuable for the more or less luxuriant ground cover. This changes with the course of succession from firegrass, fireweed, and other pioneers to the characteristic mixed layer communities of the mature aspen subclimax. The latter exhibits three chief grazing types, herb, grass, and shrub, of which the first is the most common and the second the most valuable. The pine communities which regularly indicate burns are lodgepole and knobcone forests. The subclimax of lodgepole, *Pinus contorta*, is much the most extensive and important, occurring in both the montane and subalpine zones of the Petran and Sierran regions. The community of knobcone pine, *Pinus attenuata*, is a similar fire subclimax, but it is confined to southern Oregon and California. In the Rocky Mountains, the mature lodgepole forest is almost completely without a ground cover, and hence possesses almost no grazing value. In its earlier stages, herb and grass associes are well-developed, and for a time aspen scrub may form a typical stage. In the Coast forest, *Pseudotsuga* and *Larix* are fire indicators and their communities exhibit herb and shrub layers in the early stages especially.

CARRYING CAPACITY.

Nature and significance.—The practical measure of the value of a range is its carrying capacity. By this is meant the number of animals which can be grazed upon it, expressed in terms of unit area, such as the number of head grazed upon a section (640 acres), or the number of acres required to support a single animal. It is usually expressed in terms of cattle as a basis, though it is better to indicate it in terms of the animal to which the range is best adapted, especially in the case of mixed grazing. As used at present, carrying capacity is only a relative measure of the food value of a range or type. This is due to several facts which introduce elements of uncertainty. Few grazing types are uniform, either in density or composition, and the utilization of any dominant depends to a great extent upon its associates. Even greater variation in carrying capacity results from annual fluctuations in rainfall. On the animal side, each kind of stock has its own preferences, as that of cattle for grass and sheep for herbs, while horses and sheep utilize a forage cover much more completely than cattle. Similar great differences result from the methods of handling stock, especially with reference to the manner of herding by ages or classes, or in the open or band system, with respect to water, salting, etc. Carrying capacity may vary significantly with the breed of stock, and it is obviously affected by winter feeding in regions of year-long range. Finally, perhaps the largest element of uncertainty lies in the great variation in the size and condition of stock when turned off of the range. As a consequence, it is clear that more exact measures must be introduced, which will permit an accurate comparison of different ranges and at the same time furnish a guide to the varying conditions of the same range. The Forest Service (Jardine and Hurtt, 1917) has already done much in this connection, especially with respect to the extensive measurement of carrying capacity, while the Office of Dry-Land Agriculture (Sarvis, 1919) has developed a basic method of intensive measurement. By the proper combination of these two methods, it will be possible to secure an exact measure of the carrying capacity of all grazing types, as well as of the fluctuations from year to year and under different kinds of management.

Determining factors.—With respect to the plant cover alone, the carrying capacity of a grazing type is summed up in the total amount of the annual crop of forage. But the total yield must be interpreted in terms of value and utilization. Hence, it is necessary to take into account the composition of the type, the palatability and nutritive value of the dominants and subdominants, the duration and timeliness of the grazing season, and the effects of the climatic cycle. Most of these factors are susceptible of exact measurement, particularly the structure and yield of each type, the chemical composition of the dominants, and the response to annual variations in rainfall. Their practical significance, however, is subject to the test of actual grazing, and hence it is imperative to take into account the relation of each to the type of grazing indicated by the community. All of these relations are summed up in grazing management, in which the kind of stock, the organization of the range, and the method of handling are the determining factors. These are determined by the kind and amount of the annual yield of forage, and in turn react decisively upon it. They are considered briefly in the fol-

lowing paragraphs, while their part in overgrazing is discussed in the next section, and their relation to increased carrying capacity under that dealing with range improvement.

Relation to communities and dominants.—The general value of climax and seral communities as grazing indicators has already been discussed. This is related directly to the carrying capacity, which is determined by the nature of the dominants and subdominants and their groupings. The value of a dominant is determined primarily by its total yield, palatability, and nutrition content, but it is affected in the most striking fashion by associated dominants. In fact, palatability is regularly the controlling factor, since a grass of high yield and nutrition content may remain untouched in a community of more palatable species, while it may be completely utilized when forming a pure community or in the absence of more succulent forage. Thus, the question of relative palatability becomes of the first importance in the study of overgrazing and of range improvement. It varies with the kind and breed of stock, with the phases of the climatic cycle, and with the year or season.

With respect to total yield, the relative importance of dominants may be best illustrated by the grassland climax. The tall-grasses produce more forage than the short-grasses, and the sod-grasses more than the bunch-grasses; but a tall bunch-grass, such as *Agropyrum spicatum* or *Andropogon halii,* may yield more heavily than a short-grass like *Bouteloua gracilis,* though the latter is more palatable and hence more completely utilized. A short-grass like *Bulbilis,* which forms a compact turf, has a higher carrying capacity than *Bouteloua gracilis* with an open turf, while the latter excels the more open *B. eriopoda* as well as the bunch-like *B. rothrockii.* A mixed community of tall- and short-grasses has much the highest carrying capacity of all, and of these the most productive is one in which the lower layer is *Bulbilis.* Subdominants which approach the grasses in palatability have a similar rôle in increasing carrying capacity, but the great majority are less palatable and decrease the yield in proportion to their luxuriance. Grasses also affect the carrying capacity by virtue of different times of development. A community which contains *Stipa spartea* or *comata* permits earlier grazing than others, while a mixed prairie with *Stipa, Agropyrum,* and short-grasses not only affords the longest season, but likewise the most continuous production of forage. The relative yield of tall- and short-grasses is also affected by the rainfall of wet and dry periods. The yield of tall-grasses seems to be reduced proportionately more than that of short-grasses by a drought period and is correspondingly greater during a wet period (plate 35).

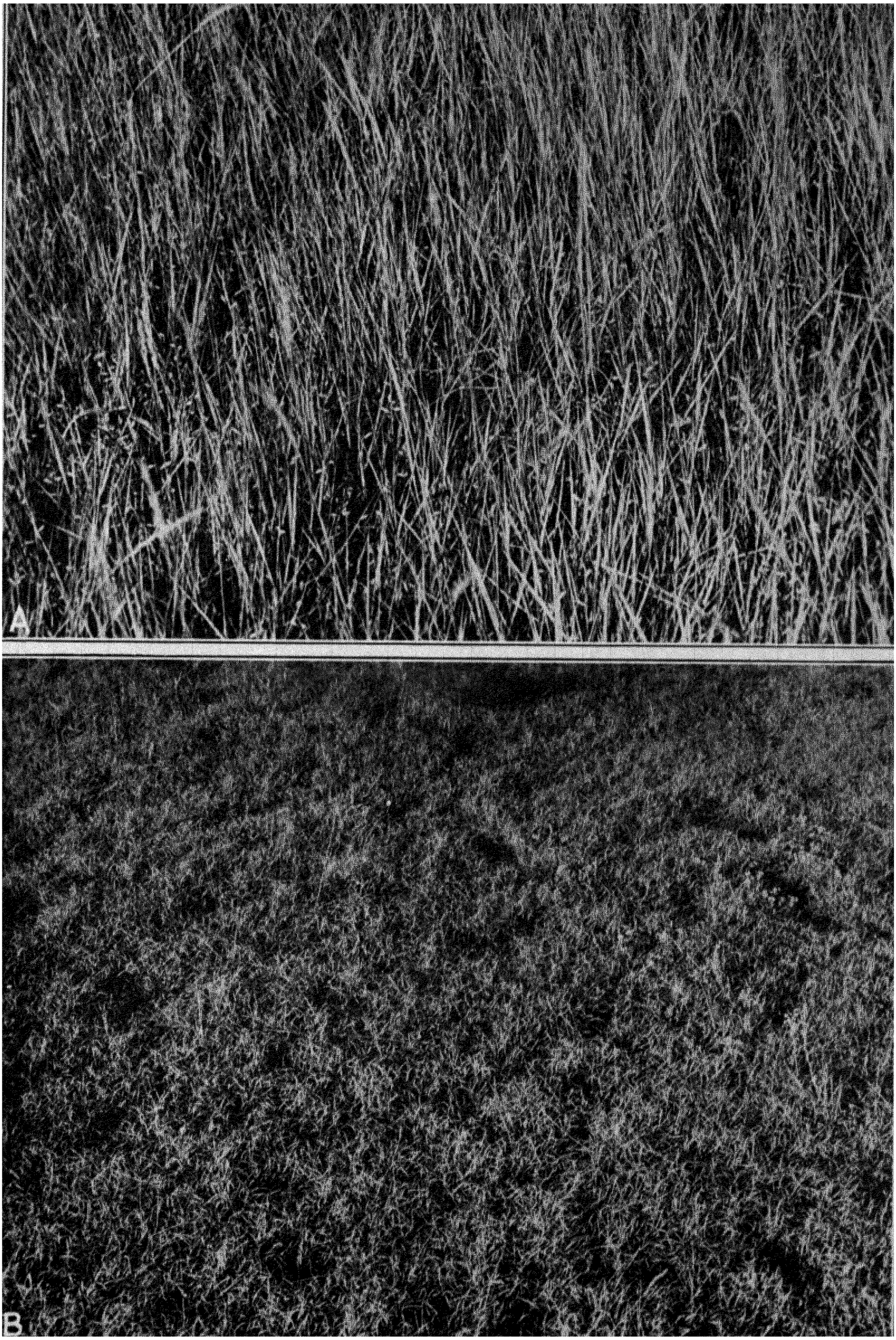
The relation of grouping to palatability is perhaps best seen in the mixed prairie and true prairie, though it exists in all communities where two or more dominants differ in this respect. In general, *Stipa comata* is most readily eaten, *Agropyrum glaucum* slightly less so, and *Andropogan scoparius* little or not at all, when they occur in mixture or as althernes. As a consequence, *Stipa* is often eaten out or kept down to such an extent that it fails to fruit. In its absence *Agropyrum* bears the brunt of the grazing and sooner or later decreases to a marked degree, thus making the short-grasses more available. In spite of their high value, the latter are less succulent and seem to be less palatable during the growing season. It is only after *Stipa* and *Agropyrum* have

disappeared and the short-grasses have been grazed closely that *Andropogon* is brought into requisition. Under such conditions, which obtain frequently during drought periods, it is grazed fully as closely as the other grasses are normally. In ordinary years a similar result can be secured by burning the dead stems and keeping the bunches grazed while they are green. The relation of *Koeleria* to its associates is less clear, yet the fact that it is often present but rarely dominant, combined with its early growth and succulence, suggests that it resembles *Stipa* in being grazed heavily.

With reference to the dominants, conditions are similar in the true prairies, except for the absence of the short-grasses. Differences in palatability are expressed chiefly in the emphasis of the subdominants, with the result that they often exceed the grasses in total yield. Practically all the herbs are inferior to the grasses in palatability, and they are lightly grazed as a rule, until the grasses have begun to disappear. Various stages of this process are seen in pastures, the more palatable species dropping out first, followed by those less and less palatable until only the most unpalatable ones, such as *Solidago, Artemisia, Verbena,* etc., remain as indicators of overgrazing. The desert plains have a large number of dominants and a corresponding number of groupings. As a consequence, differences in palatability play a decisive part in them also. The species of *Bouteloua* are most readily eaten, those of *Aristida* less readily, while *Andropogon* and *Heteropogon* are eaten little or not at all until the supply of the others runs low. As a result, the presence of *Aristida* and *Heteropogon* serves to indicate overgrazing of *Bouteloua,* while their increase may be used as a measure of the degree.

Nutrition content.—A scrutiny of the following tables will show that differences in palatability are much more important than those of nutrition content, as shown by the chemical analysis of dominants and subdominants. It is surprising to find some grasses which ordinarily are grazed little or not at all possessing as high a nutrition content as the best species of the range. It is equally surprising to find that many annuals possess apparently a higher nutritive value than related perennial species of much greater grazing value. The native grasses have much the same composition as the cultivated ones, while the sedges run higher in protein and carbohydrates than the grasses. The rushes have about the same protein content as the sedges, but are slightly higher in carbohydrate. The legumes, other herbs, and dicotyl shrubs are the highest in protein, and low in crude fiber, while the shrubs contain as a rule the species of highest fat content. The emergency forage plants, such as *Dasylirium, Nolina,* and *Yucca,* are lowest in protein and highest in crude fiber. The cacti are lowest in crude fiber, low in protein, highest in ash, in starch, sugars, etc., and in the water-content of the green plants.

The data in the tables below have been gathered chiefly from the following sources: Cassidy and O'Brine (1890), Shepard and Williams (1894), Shepard and Saunders (1901), Knight, Hepner, and Nelson (1905, 1906, 1908, 1911), Kennedy and Dinsmore (1906, 1909), Griffiths and Hare (1907), Vinson (1911), Griffiths (1915), and Wooton (1918). The table of the average composition of different groups of plants is from Knight, Hepner, and Nelson (1911:12), and that of average digestion coefficients from Kennedy and Dinsmore (1909:35).



A. Mixed prairie of tall-grass (*Agropyrum*) and short-grass (*Bulbilis*), Winner, South Dakota.

B. Pure turf of short-grass (*Bulbilis*), Ardmore, South Dakota.

GRASSES.

Species.	Ash.	Ether extract.	Crude fiber.	Nitrogen-free extract.	Protein.
	p. ct.	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
Agropyrum caninum	4.73	2.00	36.15	48.56	8.56
glaucum	8.23	2.90	34.30	44.92	9.65
scribneri	3.86	2.99	31.26	52.12	9.77
spicatum	9.90	3.02	30.84	50.09	6.15
Agrostis alba	11.40	1.61	32.17	47.82	7.00
hiemalis	7.21	3.34	31.84	49.54	8.07
Andropogon furcatus	6.66	3.19	33.81	49.35	6.99
hallii	6.52	1.97	38.70	44.87	7.94
nutans	6.94	1.70	37.64	49.54	4.17
saccharoides	7.16	1.64	36.78	48.00	6.42
scoparius	6.05	2.29	34.39	51.31	5.96
sorghum halepense	6.33	3.01	32.36	44.13	14.17
Aristida californica	8.05	0.90	34.50	50.54	6.01
divaricata	7.20	2.55	34.89	49.71	5.65
purpurea longiseta	8.10	1.42	36.87	46.18	7.43
micrantha	9.11	2.01	28.24	55.36	5.28
basiramea	10.09	2.29	16.28	67.28	4.06
Avena fatua	8.25	3.18	30.55	50.95	7.07
Bouteloua bromoides	7.64	1.87	30.94	54.84	4.71
eriopoda	10.27	1.74	33.92	48.76	5.31
gracilis	4.86	1.43	34.68	50.79	8.24
hirsuta	11.07	2.59	34.97	45.10	6.27
racemosa	9.63	1.94	32.86	49.23	6.34
rothrockii	6.53	1.58	36.67	50.55	4.67
aristidoides	6.84	2.12	35.11	46.96	8.97
polystachya	10.07	1.90	30.90	42.00	9.80
Bromus ciliatus	7.68	2.21	35.23	43.94	10.94
inermis	6.21	2.71	29.50	52.11	9.47
marginatus	7.39	1.79	35.80	44.68	10.34
hordeaceus	11.15	4.95	29.91	38.28	15.71
maximus	9.51	2.89	28.66	49.88	9.06
rubens	4.16	2.07	33.24	55.00	5.53
tectorum	23.96	3.56	24.11	29.86	18.51
Bulbilis dactyloides	10.51	2.11	25.29	54.74	7.35
Calamagrostis canadensis	6.92	2.15	34.92	46.88	9.13
purpurascens	4.34	2.35	35.52	49.29	8.50
Calamovilfa longifolia	6.39	1.82	39.59	46.14	6.06
Cenchrus tribuloides	10.96	2.15	16.69	63.62	6.58
Chloris elegans	12.93	1.96	32.19	42.44	10.48
Dactylis glomerata	10.68	3.45	27.24	44.53	14.10
Danthonia intermedia	4.68	2.56	18.71	64.57	9.48
Deschampsia caespitosa	7.21	1.57	35.75	47.84	7.63
Distichlis spicata	10.66	2.15	29.06	49.50	8.63
Echinochloa crus-galli	9.96	2.28	31.08	47.12	9.56
Elymus canadensis	8.85	2.23	34.51	46.24	8.17
condensatus	7.96	2.81	37.77	41.93	9.53
sitanion	10.10	2.27	35.61	43.21	8.81
triticoides	6.33	1.97	39.55	46.32	5.83
Eragrostis pilosa	10.10	2.44	28.79	43.44	15.23
major	14.53	2.60	17.70	56.24	8.93
Eriocoma cuspidata	8.09	2.22	32.19	48.30	9.20
Festuca ovina	6.30	2.09	35.31	50.66	5.14
scabrella	10.64	1.40	35.58	43.02	9.36
megalura	6.28	1.67	31.17	53.50	7.42
octoflora	7.44	2.47	29.45	50.49	7.15

GRASSES—*continued.*

Species.	Ash.	Ether, extract.	Crude. fiber.	Nitrogen-free extract.	Protein.
	p. ct.	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
Heteropogon contortus	6.01	1.44	33.28	54.79	4.48
Hilaria cenchroides	9.37	2.09	24.51	55.26	8.77
jamesii	8.56	2.41	31.95	48.39	8.69
mutica	8.17	1.66	32.77	50.32	7.08
Hordeum jubatum	10.83	3.39	31.90	42.40	11.48
maritimum	11.77	1.96	33.02	44.65	8.60
murinum	6.86	2.00	35.99	47.72	7.43
nodosum	5.50	2.62	30.70	49.47	11.66
Koeleria cristata	7.45	3.03	33.94	46.98	8.60
Lamarckia aurea	25.79	3.17	29.90	36.21	4.93
Muhlenbergia gracilis	5.12	2.59	25.72	59.72	6.85
gracillima	12.36	2.53	31.03	46.31	7.77
porteri	6.53	2.28	35.63	49.59	5.97
Munroa squarrosa	11.82	1.57	35.31	38.71	12.59
Panicum lachnanthum	11.96	2.38	29.97	45.72	9.97
virgatum	6.26	2.25	33.52	51.52	6.45
capillare	10.45	1.73	30.26	46.97	10.59
Phleum alpinum	4.83	2.33	32.20	51.69	8.95
pratense	7.34	1.94	37.44	46.30	6.98
Phragmites communis	7.80	2.92	35.97	44.40	8.91
Poa arctica	5.36	1.80	29.89	50.65	12.30
arida	7.14	2.58	36.76	47.90	5.62
compressa	5.74	2.97	33.73	50.31	7.25
nemoralis	6.26	2.59	31.92	51.60	7.63
nevadensis	5.05	2.06	33.68	52.17	7.04
pratensis	7.77	3.17	34.39	46.38	8.29
rupicola	4.38	2.64	26.11	58.19	8.68
sandbergii	5.09	4.11	31.43	51.07	8.30
tenuifolia	9.45	2.92	19.40	59.47	8.76
Polypogon monspeliensis	11.57	2.58	24.41	52.17	9.27
Schedonnardus texanus	7.98	1.77	38.15	45.94	6.16
Scleropogon brevifolius	8.59	2.02	30.41	51.20	7.78
Setaria glauca	13.32	4.34	16.97	55.91	9.46
italica	11.17	3.24	35.22	38.21	12.16
viridis	12.15	2.87	16.40	59.91	8.67
Spartina cynosuroides	6.16	2.25	36.79	47.16	7.64
gracilis	7.65	2.00	35.21	47.74	7.40
Sporobolus airoides	8.39	1.78	32.19	48.92	8.72
asperifolius	7.76	2.31	33.70	50.31	5.92
auriculatus	10.46	2.26	33.42	48.11	5.75
brevifolius	7.16	2.40	33.30	50.37	6.77
cryptandrus	7.05	1.57	33.49	50.03	7.86
flexuosus	6.49	1.31	34.01	51.13	7.06
wrightii	8.53	1.70	32.27	47.93	9.57
Stipa comata	6.70	2.31	34.40	49.73	6.86
eminens	6.53	2.37	38.57	45.38	7.15
setigera	8.23	1.57	36.90	47.20	6.20
spartea	4.78	2.46	23.81	60.61	8.34
vaseyi	7.80	2.77	34.08	41.80	14.05
viridula	8.04	2.61	30.87	49.77	8.71
Trisetum subspicatum	5.35	2.46	32.91	47.08	12.20
Zea mays	7.30	0.70	28.80	49.30	3.80

SEDGES, RUSHES AND HORSETAILS.

Species.	Ash.	Ether extract.	Crude fiber.	Nitrogen-free extract.	Crude protein.
	p. ct.	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
Carex aristata	6.49	2.45	31.55	49.51	10.00
atrata	5.99	2.17	29.08	50.03	12.72
aquatilis	6.81	1.44	31.84	43.74	16.17
bella	7.41	1.45	36.27	47.02	7.85
douglasii	6.24	3.09	29.74	51.87	9.06
festiva	5.71	1.79	29.04	51.09	12.37
lanuginosa	8.45	1.94	34.28	45.83	9.50
marcida	7.85	3.39	28.50	53.21	7.05
nova	5.94	2.85	31.67	47.66	11.88
pennsylvanica	9.59	2.56	27.00	44.00	16.84
rupestris	9.12	1.96	32.33	48.51	8.08
siccata	10.30	2.40	26.79	45.66	14.85
stricta	11.13	2.52	30.13	44.97	11.24
straminea	8.72	2.32	34.16	46.56	8.24
utriculata	8.03	1.61	30.84	47.28	12.24
vulpinoidea	9.43	2.18	30.93	47.25	10.21
Heleocharis acuminata	10.55	2.39	32.65	47.51	6.90
obtusa	13.30	2.73	29.41	44.47	10.09
palustris	18.62	2.14	26.94	42.79	9.50
Scirpus atrovirens	7.25	1.55	34.20	53.21	3.79
fluviatilis	10.24	1.59	29.07	48.18	10.91
lacustris	11.30	1.14	32.56	44.95	10.05
pungens	13.42	1.69	30.81	44.56	9.52
Juncodes spicatum	3.73	2.78	26.34	59.44	7.71
parviflorum	5.47	2.09	29.01	54.72	8.71
Juncus balticus	5.51	1.53	35.64	46.47	10.85
mertensianus	6.39	1.65	24.38	54.06	13.52
nodosus	9.32	1.11	31.25	45.95	12.37
parryi	6.38	1.66	25.90	49.31	16.75
tenuis	5.79	1.82	37.07	48.39	6.93
Equisetum levigatum	21.58	2.26	23.60	42.00	10.56

LEGUMES, NATIVE.

Species.	Water.	Ash.	Ether extract.	Crude fiber.	Nitrogen-free extract.	Crude protein.
Astragalus bisulcatus	....	8.23	1.42	28.76	43.90	17.69
carolinianus	....	9.09	1.34	28.00	40.23	21.34
Hedysarum philoscia	....	6.80	1.13	22.42	51.69	17.96
Lotus americanus	....	9.05	2.96	23.28	45.67	19.04
Lathyrus coriaceus	6.87	7.32	4.02	27.65	44.83	9.31
Lupinus argenteus	....	8.12	3.18	27.01	40.05	21.63
holosericeus	....	5.28	5.62	14.43	48.80	25.87
leucophyllus	....	5.12	3.64	15.76	61.64	13.84
lyalli	....	11.59	5.08	21.37	42.58	19.38
plattensis	....	9.17	1.98	17.93	57.24	13.68
rivularis	....	10.63	7.11	16.36	38.63	27.27
Thermopsis divaricarpa	....	5.71	2.87	26.93	49.32	15.17
Trifolium dasyphyllum	....	9.76	1.91	27.37	45.72	15.24
monanthum	....	9.37	6.04	18.83	41.19	24.57
parryi	....	8.42	2.59	23.78	45.17	20.04
Vicia linearis	....	7.93	1.96	27.16	40.73	22.22

LEGUMES, CULTIVATED.

Species.	Water.	Ash.	Ether extract.	Crude fiber.	Nitrogen-free extract.	Crude protein.
	p. ct.	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
Medicago sativa	....	9.96	1.33	33.34	37.67	17.70
Melilotus alba	....	10.18	2.52	23.16	44.99	19.15
officinalis	....	6.57	1.72	42.47	34.56	14.68
Trifolium hybridum	....	8.54	2.02	31.46	44.34	13.63
incarnatum	....	12.90	2.34	32.58	38.50	13.69
pratense	....	10.23	2.68	19.01	49.19	18.89
repens	....	12.34	3.19	15.70	44.97	23.80
OTHER HERBS, PERENNIAL.						
Ataenia gairdneri	6.79	9.05	4.77	25.74	46.47	7.18
Arenaria hookeri	....	15.99	1.65	28.01	48.24	6.11
Aster campestris	....	10.73	5.45	21.32	36.18	26.32
Balsamorhiza sagittata	7.12	11.83	5.71	14.17	35.70	15.44
Castilleia miniata	....	9.52	5.26	12.43	47.23	25.56
nevadensis	....	10.21	9.74	20.62	49.27	10.16
Crepis intermedia	6.74	8.81	3.37	23.47	49.19	8.44
Franseria discolor	....	20.55	4.02	11.10	43.35	20.98
Helianthella uniflora	....	9.89	6.46	17.52	48.78	17.35
Iva axillaris	....	20.62	6.36	11.60	47.07	14.35
Leptotaenia multifida	6.15	8.88	7.04	21.71	46.35	9.87
Pentstemon procerus	....	10.21	9.74	20.62	49.27	10.16
Senecio serra	....	1.25	5.07	22.11	53.60	17.97
triangularis	....	9.16	5.89	26.68	39.09	19.18
Triglochin maritima	....	17.79	2.41	27.53	33.58	18.69
Wyethia amplexicaulis	....	10.99	12.76	10.60	50.58	15.07
mollis	6.81	16.16	3.87	15.98	46.93	16.25
OTHER HERBS, ANNUAL.						
Atriplex volutans	....	18.47	.93	29.66	37.41	13.53
Brassica arvensis	....	4.47	32.78	7.77	23.31	31.67
Cleome integrifolia	....	10.12	9.00	17.00	47.04	16.84
Erodium cicutarium	....	19.04	2.11	24.13	42.35	12.37
Lactuca ludoviciana	....	12.56	7.12	14.00	47.65	18.67
Polygonum aviculare	....	5.86	2.87	20.34	52.05	18.87
convolvulus	....	2.37	3.63	14.60	70.19	9.21
erectum	....	5.59	1.80	32.11	48.11	11.39
ramosissimum	....	7.40	1.91	30.19	44.98	15.52
SHRUBS AND HALFSHRUBS, DICOTYLEDONS.						
Amelanchier alnifolia	....	8.11	10.93	14.38	50.46	16.12
Artemisia rigida	....	6.68	3.73	21.98	46.57	21.04
tridentata	....	7.08	20.95	21.99	38.81	11.17
Atriplex canescens	7.54	10.66	2.01	29.89	40.15	9.75
confertifolia	....	25.39	1.52	17.89	42.41	12.79
nuttallii	....	13.76	0.82	16.45	51.52	17.45
semibaccata	....	20.27	1.22	19.21	42.85	16.45
Eurotia lanata	....	7.61	1.61	37.56	40.41	12.81
Prunus demissa	....	11.66	13.93	20.38	45.07	8.96
Purshia tridentata	....	4.23	3.17	14.90	57.98	12.37
Ribes cereum	....	9.47	10.26	5.76	61.24	13.27
Rosa pisocarpa	....	8.37	14.04	10.18	46.91	20.50
Salix spp	....	8.34	5.60	17.74	45.53	22.79

Shrubs and Halfshrubs, Monocotyledons

Species.	Water.	Ash.	Ether extract.	Crude fiber.	Nitrogen-free extract.	Crude protein.
	p. ct.	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
Agave lechuguilla	....	8.9	1.7	32.5	52.5	4.4
Dasylirium texanum:						
Leaves	....	3.5	1.6	41.7	48.1	5.1
Stems	....	7.3	2.3	26.5	46.3	17.6
Dasylirium wheeleri, leaves	....	4.5	2.4	39.6	48.9	4.6
Nolina erumpens	....	5.6	2.8	41.8	41.2	8.6
microcarpa, leaves	....	2.9	1.5	46.6	45.3	3.7
Yucca baccata	....	7.6	1.2	34.1	53.5	3.6
glauca, leaves	....	8.8	2.8	32.7	49.3	6.4
glauca, stems and roots	....	7.3	0.8	25.2	61.0	5.7
macrocarpa	....	4.6	0.6	43.1	48.8	2.9
radiosa:						
Leaves	....	6.8	2.7	28.9	48.7	2.9
Stems	....	9.8	2.1	25.9	55.9	6.3
Cacti, Air-Dry.						
Opuntia arborescens	5.26	27.71	1.40	13.72	46.43	5.48
arbuscula	5.31	14.55	1.61	19.75	46.63	12.35
basilaris	5.08	19.98	1.90	11.75	56.52	3.77
bigelovii	5.89	15.88	1.70	17.18	54.43	4.92
chlorotica	6.03	18.80	1.85	20.55	49.21	3.56
fulgida	5.60	13.40	1.48	5.96	70.27	3.29
leptocaulis	6.15	16.85	6.45	12.33	53.29	4.93
lindheimeri	5.33	21.78	2.08	10.65	53.37	6.79
macrocentra	7.18	16.45	2.00	11.05	55.21	4.71
mammillata	6.26	16.75	1.70	15.13	54.68	5.48
phaeacantha	6.50	15.80	1.48	12.56	60.81	2.85
polyacantha	6.68	23.23	1.16	10.95	53.04	3.94
robusta	5.68	26.81	2.13	15.98	43.70	5.70
versicolor	5.96	17.49	1.58	17.85	50.84	6.28
Cereus giganteus	8.98	15.75	1.20	19.35	57.92	5.80
Cacti, Green.						
Opuntia engelmannii	77.21	4.18	0.39	2.62	14.71	0.89
fulgida	77.79	4.24	0.34	1.66	14.37	1.60
lindheimeri	80.72	4.44	0.42	2.17	10.87	1.38
robusta	89.62	2.95	0.23	1.76	4.81	0.63
spinosior	75.54	4.63	0.49	2.56	16.01	1.77
Cereus giganteus	87.31	2.20	0.17	1.44	8.07	0.81

Average Composition of Plants.

	No. of samples.	Ash.	Ether extract.	Crude fiber.	Nitrogen-free extract.	Crude protein.
A. Native.						
I. Grass-like:						
1. True grasses.						
a. Bottom lands	44	8.64	1.98	34.48	45.89	9.01
b. Bench lands	69	7.48	2.05	35.92	46.53	8.02
c. Mountains	54	5.12	2.23	33.00	49.15	10.50
2. Sedges.						
a. Bog	32	8.34	2.26	30.06	47.49	11.85
b. Dry-land	19	6.79	2.51	29.57	49.47	11.66
3. Rushes	22	6.24	1.85	31.21	50.20	10.50
II. Not grass-like:						
1. The legumes—clovers, vetches, etc.	16	8.68	2.06	25.02	44.87	19.37
2. Salt-bushes	7	14.18	1.45	28.28	41.62	14.47
2. Sagebrush, etc.	....	6.88	11.84	21.98	42.69	16.10
B. Introduced.						
I. True grasses	7	8.06	2.35	32.85	47.28	9.46
II. Other than grasses:						
1. Alfalfa, clovers, etc.	18	9.91	1.92	30.63	40.28	17.26
2. Salt-bushes, etc.	3	26.94	1.28	17.02	37.11	17.65

Average Digestion Coefficients.

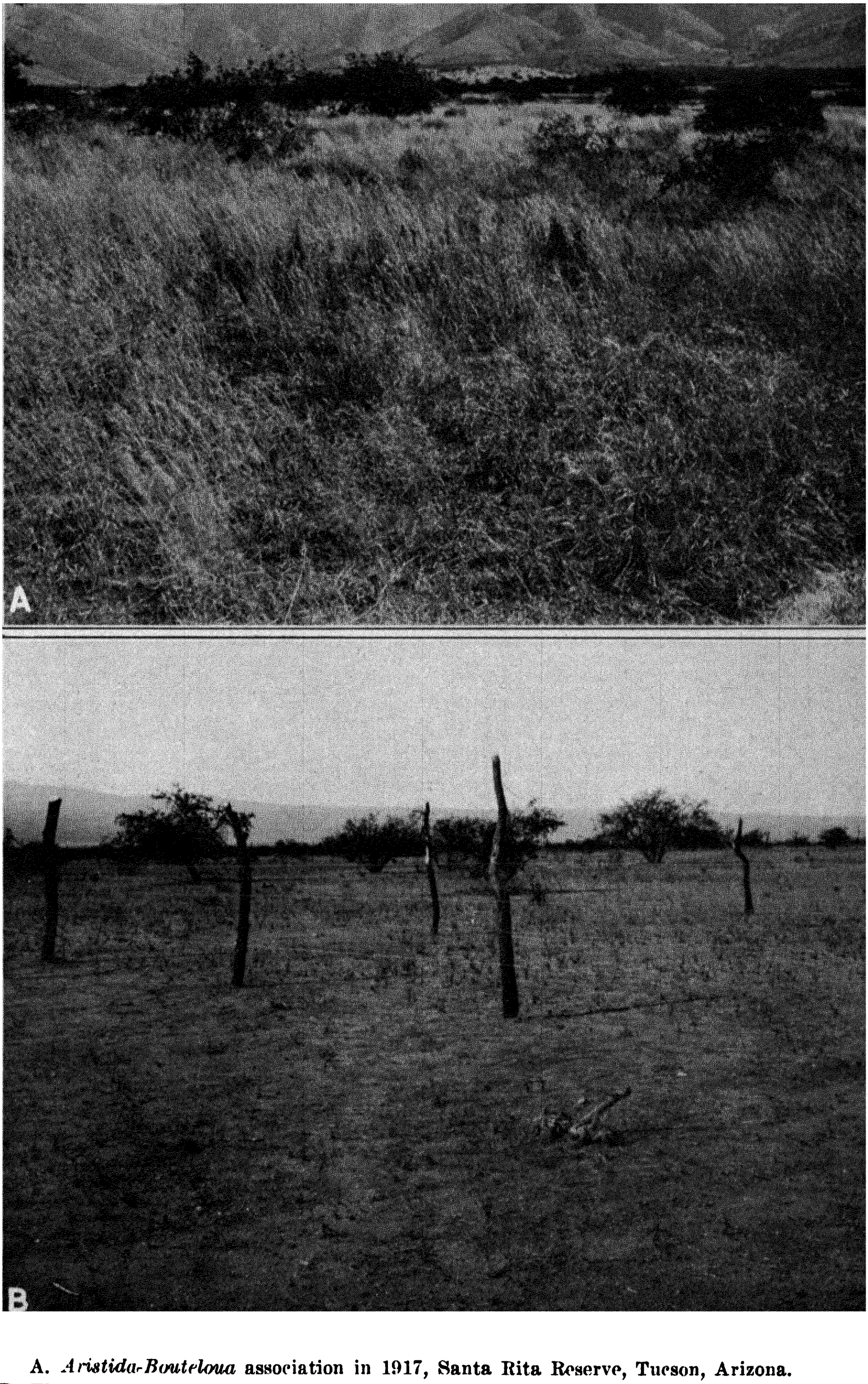
	Dry matter.	Protein.	Ether extract (fat).	Crude fiber.	Nitrogen-free extract.	Ash.	Nutritive ratio.
Indian potato (Ataenia gairdneri)	66.59	56.74	77.19	74.38	65.21	50.10	1:15.0
Common sunflower (Wyethia mollis)	60.65	69.46	63.19	54.41	61.19	53.01	1: 3.8
Balsam-root sunflower (Balsamorhiza sagittata)	66.38	77.28	74.21	58.69	74.90	38.29	1: 3.9
Wild carrot (Leptotaenia multifida)	68.76	71.10	81.49	47.39	83.04	53.07	1: 9.2
Mountain indian pink (Castilleia miniata), western variety	66.94	64.76	76.82	49.05	80.28	46.82	1: 8.9
Bromegrass (Bromus marginatus)	59.79	68.03	15.69	53.05	66.91	42.43	1: 8.5
Native bluegrass (Poa sandbergii)	52.71	63.90	49.87	44.68	60.16	22.69	1: 8.7
Dandelion (Crepis intermedia)	62.30	62.88	33.13	35.90	77.45	48.66	1: 9.5
Bitter brush (Kunzia tridentata)	76.86	81.70	71.36	69.54	86.10	57.48	1: 6.9
Bitter vetch (Lathryus coriaceus)	50.38	48.03	32.42	36.39	64.55	28.35	1: 9.4
Little lupine (Lupinus sellulus)	68.21	74.78	57.22	55.71	75.40	67.39	1: 4.2

Relation to climatic cycles.—No other factor produces such rapid and striking changes in carrying capacity as does rainfall. The difference in the total yield of the same range in two successive years of dissimilar rainfall may

be greater than 100 per cent, and in the wet and dry phase of the same cycle it may be much greater. Such differences are often greatly augmented by the critical overgrazing which is more or less unavoidable during a drought period under existing methods of management. Since grassland is typically correlated with summer rainfall, the amount of the latter is at once reflected in the growth of the dominants. A single year of deficient rainfall affects the yield at once by decreasing vegetative growth. At the same time, the storage in the propagative organs is reduced and seed production is likewise affected. If the drought continues for a second or third year, these effects become cumulative and the stand diminshes greatly in density as well as in height. During wet phases, the growth of the vegetative organs is favored and this in turn promotes propagation and reproduction, but the former especially. As a consequence, the sun-spot cycle of 11 years is clearly expressed in carrying capacity, and this is often true likewise of the 2 to 3-year cycle, particularly in the more arid Southwest. In short, grass types show a carrying capacity cycle of excess and deficit, which must be taken into account if alternate lack of utilization and overgrazing are to be avoided. Such a cycle has a peculiar significance for overgrazing and range improvement and is further discussed under these heads (plate 36).

Relation to rodents.—While the damage done by prairie-dogs to native vegetation has long been known and the indicators recognized (Pound and Clements, 1898:299; 1900:414), it is but recently that the full importance of rodents has been realized. This has led to the extensive campaigns for the eradication of rodents, organized and carried out during the last five years by the Biological Survey, and to the cooperative studies of the kind and amount of damage to different grazing types. The plans for the first of these were drawn up by the writer, and they have been carried out on the Santa Rita Range Reserve near Tucson through cooperation with the Forest Service, the Biological Survey, and the University of Arizona. The results have already demonstrated the serious and often critical effect which jack-rabbits have upon the range and have added the kangaroo-rat to the list of rodent pests of the first importance (Vorhies, 1919). While prairie-dogs, ground-squirrels, jack-rabbits, and kangaroo-rats are the most important, pack-rats and pocket-gophers also do much damage, and there are doubtless other rodents which must be reckoned with. The reduction of carrying capacity by rodents is a serious matter at all times, but it becomes critical during drought periods. This is due to its added effect upon a range which is already overgrazed by the stock. The frequent occurrence of drought in the Southwest has greatly magnified this effect, and in some areas the grass (and even the desert scrub) has been almost completely destroyed as a consequence. It is probable that there is a rodent cycle, due to the effect of dry and wet phases upon vegetation as the food-supply, but in a local area this must be more or less modified by the effects of migration. Rodents resemble grazing animals in showing a preference for certain life-forms and dominants, as well as in adjusting themselves to less palatable species under the spur of necessity. The general features of the methods by which their habits are studied and their effects measured are given under the discussion of range improvement.

Relation to herd and management.—The recognition of the proper methods of handling stock to secure the maximum carrying capacity was first made



A. *Aristida-Bouteloua* association in 1917, Santa Rita Reserve, Tucson, Arizona.
B. The same area in 1918 after serious drought and overgrazing by cattle and rodents.

supplemented by experimental tests under controlled conditions which permit varying one factor, such as grazing type or kind of animal, while the other factors remain essentially the same. Such grazing experiments may be intensive or extensive in scope, though it is desirable to make use of both kinds in connection with putting experimental results into practical commission Extensive experimentation has been carried on for several years on the Jornada and Santa Rita Range Reserves by the Forest Service (Jardine and Hurtt, 1917), while intensive experiments have been made at Mandan and Ardmore by the Office of Dry-Land Agriculture (Sarvis, 1919). Whether carrying capacity is determined by general experience or measured by actual experiment, the extension and use of the measures obtained depend upon the composition of the grazing type and the abundance and size of the dominants, as determined by the quadrat method. The degree of carrying capacity depends, first, upon the number and kind of the dominants associated in any grouping; second, upon their density; and third, upon the abundance of subdominants. Once it has been found for any particular grouping by experience or experiment, it can be extended to the same or similar types in other regions by using the dominants as indicators and checking this by means of the quadrat as a measure of composition, abundance, and yield. This is especially true where protection inclosures are employed, since they readily show the increase possible in the particular grazing type.

Present and potential carrying capacity.—The present capacity of a particular grazing type is determined by its structure and the degree to which it is overgrazed. Its potential capacity depends upon the recovery possible under proper grazing management and the increased utilization brought about by supplementary forage crops. The actual present capacity of a range is determined by the yield during drought periods, while the potential capacity is suggested by that of wet periods, which may be several times greater. While the open range in the grassland climax has been more or less locally overgrazed since the advent of the buffalo, the evidence indicates that the carrying capacity was higher for a decade or two after the disappearance of the buffalo and that it has steadily decreased up to the present time, except in the regions where settlement and fencing have brought about some degree of protection. During the last decade, the carrying capacity of ranges in the national forests has been increased 20 per cent or more as a result of grazing control, and it appears certain that the open range will permit much greater improvement. The amount of the latter will depend upon the difference between the present and the potential capacity. A mixed type of tall-grasses and short-grasses will have a higher potential capacity than one of either grass-form alone, though overgrazing may reduce its present yield practically to that of a short-grass type. The mixed prairie of North Dakota has been shown by Sarvis (1919) to have a carrying capacity of 1 to 7 during the drought years of 1917-18, while it might well equal 1 to 3 during wet periods. The short-grass type of the Texas Panhandle has an average capacity of 1 to 12 (Smith, 1899:11), while in New Mexico it seems to be somewhat lower (Wooton, 1908:27). In the desert plains, the *Bouteloua eriopoda* consociation has a capacity of 1 to 20 (Jardine and Hurtt, 1917:17), while Wooton (1916:22) assigns a similar value to the *Bouteloua-Aristida* communities of the Santa Rita Reserve. The short-grass types are grazed for a

longer period, however, and their comparative carrying capacity is relatively higher.

OVERGRAZING.

Nature.—In practice, a range is regarded as being overgrazed only when its carrying capacity has actually decreased. Such a test is often indefinite because of the conditions under which the stock industry is carried on, and this explains the divergent views as to the condition of particular ranges. While conclusive evidence as to the degree of overgrazing must be obtained from the failure of a range to maintain the herd upon it, such evidence can rarely be secured except from experimental tests. This is due to many factors, of which variations in carrying capacity with the climatic cycle and differences in management are the most important. As a consequence, it is most satisfactory to draw evidences of overgrazing from the behavior of the plant cover and to determine the degree by means of quadrat measurements. The competition between the individuals and species of the plant community is so keen and the balance so exact that the slightest disturbance can be readily detected. Grazing itself constitutes such a disturbance, and its effects upon growth, propagation, and reproduction can be minutely measured by means of the various kinds of quadrats. Such dominants as the grasses, however, have such an advantage over the subdominant herbs because of their underground parts and methods of growth that only a severe disturbance can throw the balance in favor of the herbs. When this happens, the first evidence is afforded by the increase in the number and vigor of the latter, which consequently serve as indicators. With increasing disturbance due to overgrazing, the annual members of the native flora appear in the most disturbed areas as the pioneers of minute subseres, and are later followed by introduced weeds. In the final condition the grasses will have disappeared, largely or completely, only the more weedy societies will persist, and the ground will be chiefly or wholly occupied by weedy annuals and biennials. Such a community represents one or more stages of the secondary succession and its tenure depends upon the continuance of the disturbance that initiated it. If the latter ceases, the successional process begins and soon terminates in the original climax if the grass dominants have not been killed out. Under such conditions, succession is universal and inevitable in all climaxes, and this fact lies at the basis of all methods of range improvement.

On the basis of the maximum annual production of forage, overgrazing occurs whenever the yield drops below this point. It is evident that the maximum production can not have a fixed or average value, but that it must be correlated with the periods of the climatic cycle. A degree of grazing which would be disastrous in a drought period would fall far short of adequate utilization during a wet one. Coville (Sampson, 1908:5) has applied the term "destructive overgrazing" to the condition in which all or part of the native dominants are killed. It is characteristic of areas overgrazed during the critical drought periods of the double sun-spot cycle. For the sake of clearness, three types of grazing are recognized here. These are overgrazing, close grazing, and reserve grazing. Overgrazing results when the proper maximum yield of a particular year or period is not obtained because of the failure to make enough food for propagation or seed-production, or because

the seed-crop has been destroyed. There are varying degrees of overgrazing from a slight reduction in yield to the complete destruction of the range. Close grazing is the type in which the total annual yield is utilized in such a way as to maintain the carrying capacity. Reserve grazing is the process in which part of the annual yield is held in reserve, either by means of a reserve pasture or by understocking. It constitutes an insurance against emergencies and is specially adapted to periods of drought. In actual practice, close grazing is usually preferable for the wet phases of the climatic cycle, and reserve grazing imperative for the dry phases.

Causes.—The primary cause of overgrazing is stocking the range with more animals than it can carry and still maintain its annual yield. This has been the universal method by which the stockman has maintained a title to his portion of the open range, since an overgrazed range offered little attraction to a new-comer. Overstocking has become such a general practice throughout the West, on private lands as well as upon the open range, that stockmen have almost completely lost sight of the potential carrying capacity of their ranges. A corollary of this is the practice of year-long grazing or of grazing during too long a season, with the result that the grass does not make a proper growth in the spring or fails to ripen and drop its seeds in the fall. Trampling is an inevitable concomitant of overstocking and frequently does more damage than the actual grazing, especially in the vicinity of wells and tanks. In addition, there are several important contributory causes of overgrazing. The most important of these is the drought period of the climatic cycle. The general practice of stockmen takes no account of the great variation in yield between the dry and wet phases. The interval between them usually permits the building up of the herd to the point where the range can not carry it during the dry phase. For a year or more the range is destructively overgrazed, until the herd is moved or a large portion has died. During such drought periods as those of 1893-95 and 1916-18, the range may be so damaged as to require several years to regain a fair carrying capacity and many years to permit the development of its potential capacity. The effect of rodents upon the range is essentially a matter of overstocking. A range which is carrying thousands of prairie-dogs or jack-rabbits is in effect already stocked with a considerable number of cattle. In the usual practice, however, no allowance is made for this fact, and the rodents steadily increase the damage done by the prevailing overstocking with cattle. This double effect becomes most disastrous during the drought period and frequently results in the complete destruction of the range over large areas, especially in the Southwest. The effect of fire upon the range is relatively unimportant by comparison, but it does sometimes do serious damage to the short-grass and desert plains by killing the rootstocks, particularly during dry seasons or dry years.

Indicators of overgrazing.—In grassland and scrub practically every species may serve as an indicator of overgrazing. This is true also of herbs and shrub associes, especially those of the subsere. In the case of woodland and forest the dominants can act as indicators only in the seedling or sapling stage, but the herbs and shrubs may indicate overgrazing as clearly as in other communities. The primary basis of overgrazing indicators lies in the fact that at any particular stage some species are eaten and others are not. Thus, at

any time the degree of overgrazing can be determined from both sets of plants. The best method consists in using one set as positive indicators of excessive grazing, and the other as a check upon these results; but in actual practice the most convenient indicators are naturally those that are not eaten. In any community such relict indicators owe their importance in the first place to the fact that the more palatable species are eaten down, thus rendering the uneaten ones more conspicuous. This quickly throws the advantage in competition to the side of the latter. They receive an increasingly larger share of water-content and light, and their growth increases accordingly. This leads to greater storage in the propagative organs as well as to larger seed-production. At the same time, the grazed species are correspondingly handicapped in all these respects, and the gap between herbs and grasses, for example, constantly widens. With the increase of the less palatable species, especially when they are bushy, the grasses are further weakened by trampling. This soon produces small bare spots which are colonized by annual weeds or weed-like plants. The latter set up a new and intense competition with the grass survivors, and these are still further decreased as a result. The weed areas widen, and sooner or later come to occupy most or all of the space between the relict herbs or half-shrubs. Before this condition is reached, however, the latter are brought into requisition for grazing and they then begin to yield to the competition of the annuals. In the case of the severest overgrazing, they too finally disappear, unless they are woody, wholly unpalatable, as in *Gutierrezia,* or thoroughly protected by spines, as in *Opuntia.*

In the grassland climax, where the effects of overgrazing have been most studied, it is possible to recognize three or four stages. The first is marked by the decrease or disappearance of *Stipa* or *Agropyrum,* or of both of them, and the corresponding increase of the short-grasses wherever these are associated; the second stage is characterized by the greater vigor and abundance of the normal societies, as well as by the increased importance of some; the third stage begins with the replacement of the grasses by annuals, while the fourth is marked by the spread of annuals and of introduced weeds generally over the area. Not all of these necessarily occur in the same spot, especially when the process of overgrazing takes place rapidly. Destructive overgrazing may result in a few years, or even in a single year, and in such instances the native vegetation may disappear completely or nearly so. It is replaced by a pioneer associes of native and introduced weeds, whose persistence will depend upon the continuance of the disturbance. These four stages indicate so many primary degrees of overgrazing, while minor degrees are denoted by the dropping out of particular dominants or subdominants. Thus in the mixed prairie, *Stipa* drops out before *Agropyrum,* because it is grazed more heavily in spring, and *Bouteloua* disappears from the desert plains before *Aristida,* owing to its greater palatability. Palatability is the chief factor in determining the successive disappearance of species, and hence the indicators of the corresponding degrees of overgrazing, though the sequence is often disturbed by the vigor of certain dominants. Since there are few species that are wholly unpalatable or inedible, it becomes possible to construct for a particular community a complete sequence of indicators, reflecting each appreciable degree in the process of overgrazing. In severe periods of drought, overgrazing may reach the point where even the annuals are eaten out and the

A. *Aristida purpurea* and *divaricata* indicating moderate overgrazing on *Bulbilis* plains, Texhoma, Oklahoma.

B. An annual, *Lepidium alyssoides*, indicating complete overgrazing in a pasture, Fountain, Colorado.

plant covering vanishes completely. This happens regularly in pastures, corrals, and bedding-grounds where animals are kept in masses. It has even been found in desert scrub and savannah where the effects of overgrazing are supplemented by the work of kangaroo-rats (plate 37).

Societies as indicators.—The number of overgrazing indicators for the several climaxes is legion, and it is possible to consider only the most widespread and important. With the perennial grasses as a background, it is convenient to distinguish several groups of such indicators, namely, herbs, subdominant halfshrubs, cacti, seral annuals, introduced weeds, and shrubs. The first three groups comprise the characteristic relict indicators, and for the most part mark the early stages of overgrazing. The annuals and weeds are typical of the later and final stages, while the shrub indicators are typical of savannahs and other ecotones where grass and scrub mix. The increased importance of societies marks the beginning of overgrazing in those associations where they are regularly present. These consist for the most part of climax herbs, but subclimax half-shrubs and grasses, such as *Gutierrezia* and *Aristida*, are often of especial significance. Moreover, many of the herbs, though regularly present in the climax, have subclimax qualities also, as is readily understood from their competitive relations to the grasses. Practically all the societies listed under the various associations of the grassland, as well as those of the other climaxes, have some value as indicators of overgrazing. In most cases this value is overshadowed by that of the most controlling and extensive societies, and the latter alone need to be taken into account.

In the following list the general order is that of importance, but this naturally varies with the locality and the season. The composites and other late-blooming species are especially serviceable, owing to their persistence.

Artemisia gnaphalodes.
Artemisia dracunculoides.
Artemisia canadensis.
Grindelia squarrosa.
Solidago rigida.
Solidago missouriensis.
Solidago speciosa.
Solidago canadensis.
Solidago mollis.
Liatris punctata.
Liatris scariosa.
Liatris spicata.
Liatris pycnostachya.
Lepachys columnaris.
Kuhnia glutinosa.
Malvastrum coccineum.
Vernonia fasciculata.
Vernonia baldwinii.
Achillea millefolium.
Helianthus rigidus.
Carduus undulatus.
Senecio douglasii.
Aster multiflorus.
Aster oblongifolius.
Aster sericeus.
Senecio aureus.
Balsamorhiza sagittata.
Balsamorhiza deltoidea.
Psoralea tenuiflora.
Psoralea argophylla.
Petalostemon candidus.
Petalostemon purpureus.
Amorpha canescens.
Amorpha nana.
Dalea laxiflora.
Tradescantia virginiana.
Verbena stricta.
Verbena hastata.
Glycyrhiza lepidota.
Brauneria pallida.
Chrysopsis villosa.
Lygodesmia juncea.
Aragalus lamberti.
Polygala alba.
Antennaria dioeca.
Astragalus mollissimus.
Astragalus bisulcatus.
Astragalus racemosus.
Astragalus crassicarpus.
Lupinus plattensis.
Erigeron ramosus.
Haplopappus spinulosus.
Hymenopappus tenuifolius.
Rosa arkansana.
Euphorbia corollata.
Salvia azurea.
Asclepias verticillata.
Monarda fistulosa.
Baptisia leucophaea.
Castilleia sessiliflora.
Allium canadense.

Halfshrubs as indicators.—Halfshrubs are best developed in the Southwest, where they are typical indicators of overgrazing in both the desert scrub and the desert plains. A few attain even greater importance in the short-grass plains and the mixed prairies. These are *Gutierrezia sarothrae, Artemisia frigida,* and *Yucca glauca.* The relation of the first two to grazing in a short-grass cover has been shown by Shantz (1911:42). Over the central

portion of the Great Plains they are associated as the two most serviceable and universal of overgrazing indicators. *Artemisia* is more abundant to the northward, and *Gutierrezia* to the southward, but they indicate essentially the same conditions whether alone or mixed. Differences in the degree of overgrazing are designated by variations in the density and vigor of the plants. In rough or sandy regions *Yucca glauca* is an indicator of overgrazing, though it is less important than the two just mentioned, largely because the flower-clusters are often eaten by cattle. *Eriogonum microthecum* and its variety *effusum* are common indicators in the central Great Plains, especially in more sandy areas or in sandhills. *Eriogonum jamesii* is even more frequent in a similar rôle, though it is barely shrubby.

Gutierrezia is also the most important indicator of overgrazing in the eastern portion of the desert plains and in the *Larrea-Flourensia* scrub. In western Mexico and Arizona it is largely or completely replaced by *Isocoma coronopifolia* and its varieties, which are the characteristic indicators from the lowermost *Prosopis* valleys upward into the *Bouteloua-Aristida* grassland. On the *Parkinsonia-Cereus* bajadas and hills, *Franseria deltoidea* is the indicator on lower slopes and *Encelia farinosa,* or more rarely *Chrysoma laricifolia,* on the upper, while *Franseria dumosa* and, to a less extent, *Hilaria rigida,* play a somewhat similar rôle in the *Larrea* plains of western Arizona and adjacent California. In the higher desert plains, *Calliandra eriophylla* and *Eriogonum wrightii* largely replace *Isocoma* as the most important indicator, while *Baccharis wrightii* is more local. Other halfshrubs that occur through the desert scrub in varying importance are *Zinnia pumila, Psilostrophe cooperi, Krameria glandulosa, Bebbia juncea,* and *Hymenoclea salsola.* While all of the halfshrubs of the desert scrub and grassland are normally indicators of overgrazing, they follow the rule in that practically every one is grazed to some degree when more palatable forage is lacking. This is altogether exceptional in the case of *Gutierrezia, Isocoma,* and *Franseria,* but all of these were found to be grazed more or less during the severe drought of 1918.

Cacti as indicators.—Cacti owe their value as indicators of overgrazing to the protection afforded by their spines. Under ordinary conditions this is almost complete protection, but during drought periods in the Southwest, cattle in particular make much use of cacti and often keep alive upon them as an exclusive diet. At such times they are utilized by jack-rabbits and pack-rats also, and the work of these rodents frequently renders the prickly pears and barrel cacti available for stock. The cacti which serve to indicate overgrazing belong almost wholly to the genus *Opuntia* (plate 38, A). The species with flat joints are commonly known as prickly pears, and those with cylindric ones as chollas. In the short-grass plains and mixed prairies *Opuntia polyacantha* and *O. mesacantha* are the chief indicators, while *Opuntia arborescens* is often the most important species from the Arkansas Valley southward. Both owe their abundance as much to the great ease of propagation as to their spiny protection. In the case of the chollas especially the joints are readily broken off and carried about by cattle, and in addition they are blown off by the wind. Moreover, they are well adapted to ecesis in disturbed places, owing to their succulence and the shallow root-system. In the Southwest the most important cactus indicators in the desert scrub and savannah are *Opuntia fulgida, O. f. mammillata,* and *O. spinosior* among the chollas, and *O. engel-*

mannii, O. discata, and *O. phaeacantha* among the prickly pears. All these extend up into the grassland to some degree at least, but in the foothills the most common species are *Opuntia versicolor, O. arbuscula, O. bigelovii,* and *O. chlorotica. Nolina, Dasylirium,* and *Agave* resemble the cacti more or less in indicator value.

Shrubs as indicators.—The shrubs that indicate the overgrazing of grassland are chiefly such dominants of sagebrush, scrub, or chaparral as mix with the grasses to form savannah. The most important are *Artemisia, Prosopis, Acacia, Yucca, Quercus,* and *Adenostoma.* They resemble each other in that grazing gives them the advantage in competition with the grasses, partly by decreasing the hold of the latter through eating and trampling, and partly by disseminating the seeds and rendering their germination more certain. This advantage is largely or completely lost in the case of browsing animals, such as goats, since all of these are readily browsed, with the exception of *Yucca* and *Arctostaphylus.* Species of *Artemisia* are the chief shrub indicators of overgrazing in the mixed prairies, short-grass plains, and *Agropyrum* bunch-grass prairie, though various dominants of the chaparral not infrequently assume this rôle also. The most widespread and important is *Artemisia tridentata,* while *A. cana* is perhaps the most common in the mixed prairies and *A. filifolia* in sandy areas and sandhills. The lower forms, such as *A. trifida, A. arbuscula, A. rigida,* and *A. spinescens,* might well be regarded as halfshrubs. They are more or less widely distributed, but their contact with grassland is more local. In California, fragments of savannah composed of *Artemisia californica* and *Stipa* indicate a similar relation between sagebrush and grassland. This appears to have been true formerly of *Adenostoma* as well, but the observed contacts with *Stipa* grassland are as yet too few for certainty. In the desert plains, *Prosopis,* often with *Acacia* or *Celtis,* is the characteristic shrub indicator of overgrazing. It also extends northward in the short-grass plains to southern Colorado and Kansas. It is perhaps the most typical of all such indicators, owing to its height and the ready dissemination of its seeds by cattle. *Quercus virens, Q. breviloba,* and *Q. undulata,* as well as other members of the chaparral, take similar parts in the grassland of southwestern Texas and adjacent New Mexico. The rôle of *Yucca radiosa* and *macrocarpa* as indicators of overgrazing is somewhat less clear, but their constant occurrence in the sandy grasslands of the Southwest and the connection between their propagation and disturbance by cattle seem to leave little doubt of a similar correlation.

Annuals as indicators.—Annuals are typically indicators of serious disturbance, and hence serve to mark the existence of serious overgrazing when abundant. They are the universal pioneers of secondary successions, and they regularly disappear in the course of development. When the disturbance is continuous or recurrent, they may persist for years, but their seral nature is readily disclosed by protecting an area. In a few cases they become suppressed by the perennials and continue as a dwarfed ground layer. In the Southwest the winter rains permit a characteristic development of annuals, which complete their growth and mature their seeds before the perennial communities of the summer become controlling. Annuals usually first appear in spots denuded by trampling and extend from these throughout the community in proportion to the degree of overgrazing. Their mobility is

often very great and they may take more or less complete control of a badly overgrazed range in a few years. Indications of varying degrees of overgrazing are given by differences in species as well as in density and vigor. The first annuals to appear are native species, or subruderals, which are given a chance to spread or develop because of the trampling and overcropping of the climax dominants. These often give way to more vigorous subruderals, or they become mixed with introduced weeds or ruderals, and are sometimes completely replaced by them. This is usually only when the disturbance has been long continued and the supply of ruderals maintained by the presence of man. In the case of complete replacement, such as by *Avena* or *Bromus,* fire has often played an effective part. When more palatable species have disappeared, annuals often furnish considerable grazing, though it is usually inferior in all respects to that afforded by the climax dominants displaced. *Avena fatua* is an exception to some extent, while in the Southwest the winter annuals are extremely important in tiding over the cattle until the summer grasses appear.

There are several hundred annuals which serve in some degree as overgrazing indicators. The most important ones are found chiefly in the grassland climax and its contacts with the scrub formations. Some of these extend upward into the grasslands of the montane zone, while the indicators of overgrazing in the higher zones usually belong to the same or similar genera. A few of the annual indicators extend more or less throughout the grassland formation, but most of them occur in their particular region. Hence, it seems most convenient to group them under the three heads, namely, prairies and plains, desert plains, and bunch-grass prairies.

Prairie and plains indicators.—While different species of annuals indicate small differences in the degree of overgrazing, the abundance and height of the plants is usually of greater importance. In addition, annual indicators have received little quantitative study, and hence it is possible only to list them in the general order of their importance. Some of those listed are either annual or biennial, and a few are typically biennial.

Plantago patagonica.
Festuca octoflora.
Hedeoma hispida.
Lepidium intermedium.
Lepidium alyssoides.
Lepidium ramosum.
Lappula texana.
Verbena bracteosa.
Helianthus petiolaris.
Helianthus annuus.
geron canadensis.
geron divergens.
geron ramosus.
opodium leptophyllum.
opodium album.
anum annuum.
anum cernuum.
Eragrostis pilosa.
Eragrostis major.
Ambrosia artemisifolia.
Salsola kali.
Solanum rostratum.
Argemone platyceras.
Dysodia papposa.
Hordeum jubatum.
Schedonnardus texanus.
Munroa squarrosa.
Euphorbia marginata.
Croton texensis.
Collomia linearis.
Verbesina encelioides.
Orthocarpus luteus.
Polygonum aviculare.
Polygonum ramosissimum.
Aster tanacetifolius.
Aster canescens.
Phacelia heterophylla.
Allionia linearis.
Cassia chamaecrista.
Coreopsis tinctoria.
Salvia lanceolata.
Lupinus pusillus.
Lotus americanus.
Draba caroliniana.
Myosurus minimus.
Androsace occidentalis.
Pectis angustifolia.
Sophia pinnata.
Physalis lobata.
Solanum triflorum.

ert plains indicators.—These fall into two groups, depending upon time of appearance. The summer annuals correspond to those listed. They occur with the grasses, and hence are a more exact measure of grazing than the winter annuals. Most of them are distributed through- the region, but are more typical in New Mexico. The winter annuals

develop most abundantly in overgrazed areas also, but they finish their growth before the grasses appear and hence indicate conditions of the previous year. They are characteristic of southern Arizona and adjacent Mexico. The most important ones, such as *Plantago fastigiata, Eschscholtzia mexicana, Lesquerella gordoni, Lepidium lasiocarpum, Pectocarya linearis*, etc., often form a dense cover and are invaluable for spring grazing.

SUMMER ANNUALS.

Aristida bromoides.	Kallstroemia brachystylis.	Haplopappus gracilis.
Bouteloua aristidoides.	Kallstroemia hirsutissima.	Eriogonum abertianum.
Bouteloua polystachya.	Cladothrix lanuginosa.	Eriogonum polycladum.
Boerhavia torreyana.	Croton corymbulosus.	Pectis angustifolia.
Boerhavia intermedia.	Solanum elaeagnifolium.	Pectis prostrata.
Kallstroemia grandiflora.	Tribulus terrestris.	Chloris elegans.
Kallstroemia parviflora.	Portulaca oleracea.	Eragrostis pilosa.

WINTER ANNUALS.

Plantago fastigiata.	Daucus pusillus.	Malacothrix sonchoides.
Eschscholtzia mexicana.	Erodium cicutarium.	Malacothrix fendleri.
Lesquerella gordoni.	Erodium texanum.	Oenothera primaveris.
Lepidium lasiocarpum.	Phacelia distans.	Calandrinia menziesii.
Pterocarya linearis.	Phacelia crenulata.	Baeria gracilis.
Bowlesia lobata.	Lupinus sparsiflorus.	Lappula texana.
Plagiobothrys arizonicus.	Thelypodium lasiophyllum.	Festuca octoflora.
Amsinckia tessellata.	Thysanocarpus curvipes	Gilia gracilis.
Sophia pinnata.	Lotus humistratus.	Salvia columbariae.

Bunch-grass prairie indicators.—The most remarkable development of annual indicators of overgrazing has taken place in California. This is undoubtedly a consequence of its early settlement, together with its mild climate and winter rainfall. In addition to a large number of summer and winter annuals derived from the native vegetation, the most widespread and typical indicators are European weeds, which are nearly all grasses. Many of these were probably introduced from Europe during the period of Spanish occupation, and spread rapidly as a result of overgrazing and fire. These agencies would have first brought about the replacement of the native *Stipas* (plate 38, B), but sooner or later fire and clearing would have caused weeds to spread through much of the chaparral as well. This problem of successive invasions and replacements is now under investigation by means of permanent protected quadrats. Meanwhile, the conclusions reached by Davy (1902:38) afford the best summary of the probable course of development:

"1. The primitive forage plants were the 'bunch-grasses' (*Danthonias, Stipas, Melicas, Poas* and perennial *Festucas*), with annual and perennial clovers, wild-pea vines and wild sunflowers; these were much more abundant in former times than now, and on account of their palatableness they largely disappeared with overstocking.

"2. With the advent of white settlers and their domestic animals, wild oats (*Avena fatua*) and alfilerilla (*Erodium cicutarium*) took possession of the country; these increased in relative abundance as the native forage plants became scarce; as the latter diminished in quantity, the cattle took to eating the former until they in like manner succumbed, while other plants took their place.

"3. Small barley grass (*Hordeum maritimum gussoneanum*), squirrel tail (*Festuca myurus*), and soft chess (*Bromus hordeaceus*) were among the next weedy introductions; the two former, when in a maturing condition being

disliked by cattle, have had a chance to spread and cover the ranges; but cattle having acquired a taste for soft chess, it is being kept in check, if not diminishing, on closely grazed ranges.

"4. A third immigration is now taking place, in which musky alfilerilla (*Erodium moschatum*), broncho grass (*Bromus maximus gussoni*), barley grass (*Hordeum murinum,* locally called fox-tail), tacalote (*Centaurea melitensis*), hawkbit (*Hypochaeris glabra*), bur-clover (*Medicago denticulata*), and other weeds are establishing themselves along the roadsides and around ranch houses. Of these, the bur-clover and musky alfilerilla have some forage value. Barley grass is eaten green in the spring before heading out, but afterwards becomes one of the most objectionable weeds for a stock range. The other aliens are destined to cause irreparable injury to the ranges unless kept in check and prevented from becoming firmly established."

With few exceptions the species listed below are summer annuals. The winter annuals of southern California are largely those noted for the desert plains, but they are here relatively unimportant. It should be borne in mind that, while the indicators given originally denoted overgrazing, some of them, such as *Avena* and *Erodium,* have become valuable forage plants as a consequence of the displacement of the native bunch-grasses, and in turn their overgrazed condition is indicated by still more weedy invaders.

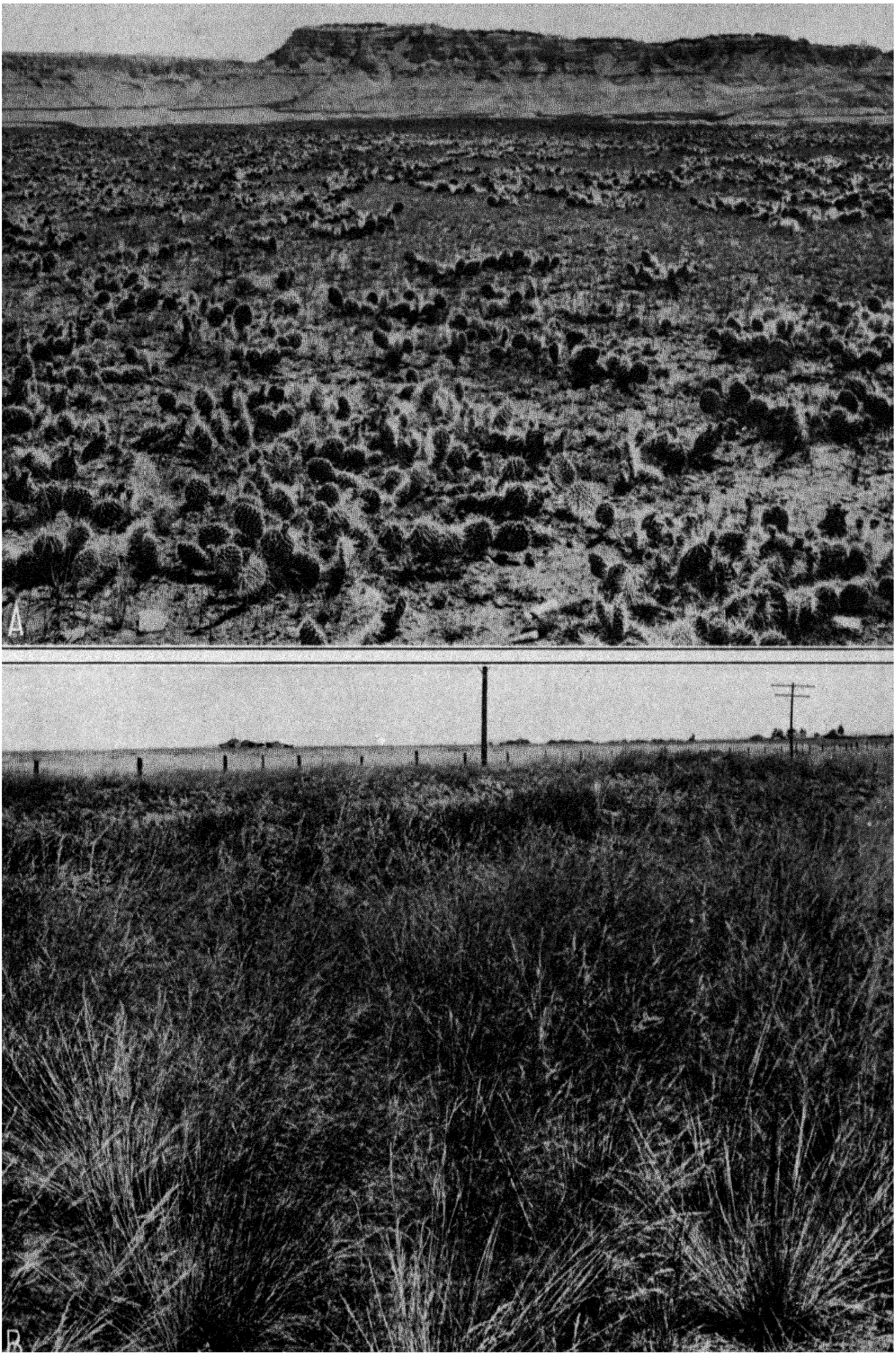
GRASS INDICATORS.

Avena fatua.
Bromus maximus.
Bromus rubens.
Bromus hordeaceus.
Bromus tectorum.
Festuca myurus.
Hordeum maritimum gussoneanum.
Hordeum murinum.
Polypogon monspeliensis.
Lamarckia aurea.

HERB INDICATORS.

Erodium cicutarium.
Erodium moschatum.
Centaurea melitensis.
Medicago denticulata.
Hypochaeris glabra.
Hypochaeris radicata.
Eriogonum vimineum.
Eriogonum nudum.
Lupinus micranthus.
Lupinus affinis.
Lupinus truncatus.
Trifolium microcephalum.
Trifolium amplectens.
Trifolium gracilentum.
Trifolium tridentatum.
Medicago lupulina.
Melilotus indica.
Raphanus raphanistrum.
Eryngium vaseyi.
Hemizonia fitchii.
Hemizonia clevelandii.
Madia exigua.
Madia dissitiflora.
Lotus strigosus.
Trichostema lanceolatum.
Plantago patagonica.
Epilobium paniculatum.
Phacelia heterophylla.
Lagophylla ramosissima.
Ptilonella scabra.
Orthocarpus purpurascens.
Centaurea cyanus.
Eremocarpus setigerus.
Lithospermum ruderale.
Navarretia leucophaea.

Great Basin indicators.—These are limited in the present discussion to the annuals that spread over the grassy intervals of the sagebrush, especially along the northern border where it is mixed with *Agropyrum spicatum.* While a number of the annuals of the preceding list assume this rôle along the western edge, three species of introduced weeds are more important than all others combined; these are *Bromus tectorum, Sisymbrium altissimum,* and *Lepidium perfoliatum.* These occur singly or variously mixed. The most extensive community is that of *Bromus tectorum,* while the mixed community of *Bromus* and *Sisymbrium* is almost equally important. *Lepidium* is most abundant in the Northwest, but is rapidly spreading to other regions. While they owe their establishment originally to overgrazing, fire is a large factor in their rapid spread. They have now replaced the native grasses and herbage almost completely over thousands of square miles, and have reduced the grazing value practically to that of the sagebrush alone. *Bromus* is the only



A. *Opuntia polyacantha* indicating serious overgrazing in mixed prairie, Hat Creek Basin, Nebraska.

B. Trackway relict of *Stipa setigera*, indicating the original climax prairie of California, now almost completely destroyed by overgrazing, Fresno, California.

one with any real value, and this is frequently slight. It furnishes some grazing for sheep in the spring, but quickly becomes dry and nearly worthless.

Overgrazing in the past.—The condition of the great ranges of the prairies and plains before the settlement of the West and the effect of settlement upon the grasses have long been mooted questions. It has frequently been assumed that certain grasses have disappeared with the coming of the early settlers and that others had entered to take their place. For example, it has been the almost universal opinion of farmers and stockmen that buffalo grass vanished from the prairies with the going of the buffalo and that the bluestems had come in from the East to replace it. This opinion has been shared to a large degree by scientific men. Bessey (1887:216) early noted the general relations of the grasses to cultivation and fire:

"Several entirely distinct species are popularly known as buffalo grass. All are, however, short grasses, unfit for making into hay, and although apparently quite nutritious, they supply so small an amount of food per acre that as the land becomes more valuable the farmer can not afford to retain them. But even should he wish to retain them, he can not; for they are unfitted to battle successfully with bluegrass and white clover, with the blusestems and rank weeds which always spring into prominence upon the prairies when the settler stops the annual prairie fires. Moreover, they can not endure the close cropping and trampling to which they are subjected when the land is inclosed and used for regular farming purposes. Already the genuine buffalo grass (*Buchloe dactyloides*) has practically disappeared from the eastern third of the State. Of course I know very well that there are patches of it here and there in these older counties; it may be found in such patches within a mile or two of the capitol building; but these little patches are as nothing when compared with its former extensive distribution. A second grass commonly known by the name of buffalo grass (*Bouteloua oligostachya*) is fast following the first.

"Buffalo grass, *Bulbilis dactyloides,* is widely spread throughout the Sandhill region. This valuable forage plant is rapidly disappearing. Its hard-awned fruits were especially suited for distribution by the buffalo, and since these have disappeared and the prairie fires are no longer allowed to sweep the plains, the buffalo grass is being rapidly choked out by the ranker species. It is the most valuable native pasture grass, but is rapidly passing toward extinction" (1893:288).

Webber (1890:37) states that "the buffalo grass, once the prevailing plant, is, in eastern Nebraska, found only in small patches, and is fast becoming rare," while Crandall (1890:136) says that "this, the true buffalo grass, which once formed so large a portion of the prairie turf, is now found in this region only in isolated patches."

Pound and Clements (1898:246, 1900:350) found evidence to indicate that the buffalo grass had disappeared only where the land had been broken for cultivation.

"The buffalo grass was, until recently, supposed to have once covered the greater portion of Nebraska; its disappearance has, as a matter of sentiment, been connected with that of the buffalo. That such a supposition is entirely erroneous is beyond a doubt. The patches of buffalo grass, which are found scattered here and there over the State, are to be regarded as intrusions rather than stragglers left by a retreating species."

In 1897, Williams wrote:

"This famous range grass is still quite abundant in the regions west of the James Valley in both Dakotas. It is by no means as rare as most people suppose, being frequently overlooked on account of its similarity to certain of the grama grasses and because it seldom fruits in any great quantity." (14)

In speaking of the changes accompanying overgrazing in the Texas prairies, Smith (1899:28) makes the following statement:

"Before the ranges were overgrazed, the grasses of the red prairies were largely bluestems or sage grasses (*Andropogon*), often as high as a horse's back. After pasturing and subsequent to the trampling and hardening of the soil, the dog grasses or needle grasses (*Aristida*) took the whole country. After further overstocking and trampling, the needle grasses were driven out, and the mesquite grasses (*Hilaria* and *Bulbilis*) became the most prominent species. The occurrence of any one of these as the dominant or most conspicuous grass is to some extent an index of the state of the land and of what stage in overstocking and deterioration has been reached. There is often a succession of dominant grasses in nature through natural causes, but never to as marked an extent as on the cattle ranges during the process of deterioration from overgrazing. On overstocked lands there is uniformly an alternation of needle grass and mesquite at short intervals, unless the overstocking is carried too far, when these perennials give way to annuals and worthless weeds."

Smith (1893:281) has suggested part of the explanation as to the varying opinions upon the condition of the range since the disappearance of the buffalo, in discussing the sandhills of northern Nebraska:

"The theory is quite commonly advanced by stockmen and others interested in the country that the sandhills were quite bare of vegetation at a comparatively recent date and have only commenced to be grassed over since the days of the Indian and buffalo. I doubt very much the correctness of this idea. We have accounts of the sandhills written in the early part of this century which gave the salient features of the landscape about as they exist today. The region is one where physical conditions may vary greatly in a term of years. We were told by stockmen who have been located in the hills for a long time, that the soil is very susceptible to drying, that the lakes sometimes entirely disappear during periods of drought, and that one year a crop of hay may be cut where the year before there was a fine body of water. In wet years the vegetation of the valleys, which is always more luxuriant than that of the drier hills, may extend far up their slopes, while in dry years opposite conditions may prevail. If one sees the sandhill region for the first time when bare of vegetation in winter or early spring, or after the drying out of July and August, one may easily get the idea that the sandhills have never been grassed over. When the freshening up comes after the rains, he may conclude that they are becoming turfed over for the first time."

Wilcox (1911:26) has compiled the opinions and statements of a very large number of explorers and travelers with reference to grazing conditions over the prairies and plains during the past century. These show great divergence, and many of them are directly contradictory. On the whole, however, they support the general conclusion that the range has not changed essentially, whatever its fluctuations may have been.

"The present condition of the Great Plains is essentially the same as that described by early travelers. The prevailing grasses are still the buffalo and grama, of low habit. The immense number of buffalo in the early days and

later of cattle have not been sufficient to produce any marked change in the character and amount of range forage upon this area." (47)

"To one who is familiar with the present range conditions of the arid west as a whole, or any particular section of it, these statements must indicate a striking similarity in the appearance of the range in former times and at present. So far as the numerous statements which have been consulted indicate, the general appearance and conditions of the range country have changed but little since the time when they were first explored by white men." (45)

Succession and cycles.—The range studies of the past six years have furnished a complete explanation of the sharp difference in views as to the past conditions of overgrazing. There is no question that Smith, Wilcox, and others are correct in stating that there has been no essential permanent change in the composition and structure of the great grassland associations. On the other hand, it is equally certain that there have been great local or temporary changes, which critically reduced the carrying capacity, or actually destroyed the climax community. A broad view of the grassland climax would warrant the opinion that it had never undergone serious change, while the observation of a particular range would justify the statement that the original grasses were completely destroyed. This apparent contradiction is readily explained by the student of succession, as is likewise the fact that one observer may find good grass in the same locality where another had seen a barren waste. It is obvious that an area destructively overgrazed would be abandoned by grazing animals for an untouched portion of the same climax, and that the bare area would then pass through the various stages of succession to again reach the climax in 20 to 30 years. This is recognized by Wilcox (31) in connection with the overgrazing caused by buffalo:

"These accounts indicate what would naturally be expected, viz, that where buffaloes congregated in immense herds the grass was totally destroyed for the time and the ground was much cut up or packed down, according as dry or wet weather prevailed. The result of such accumulations of large herds was the apparent total destruction of the grass. It should be remembered, however, despite the fact of apparent total destruction wrought by the buffalo along the line of their migration and during their close association at breeding seasons, the range recovered so that the evidence of their destructive grazing was entirely lost within a few years. This fact indicates also the possibility of range improvement at present."

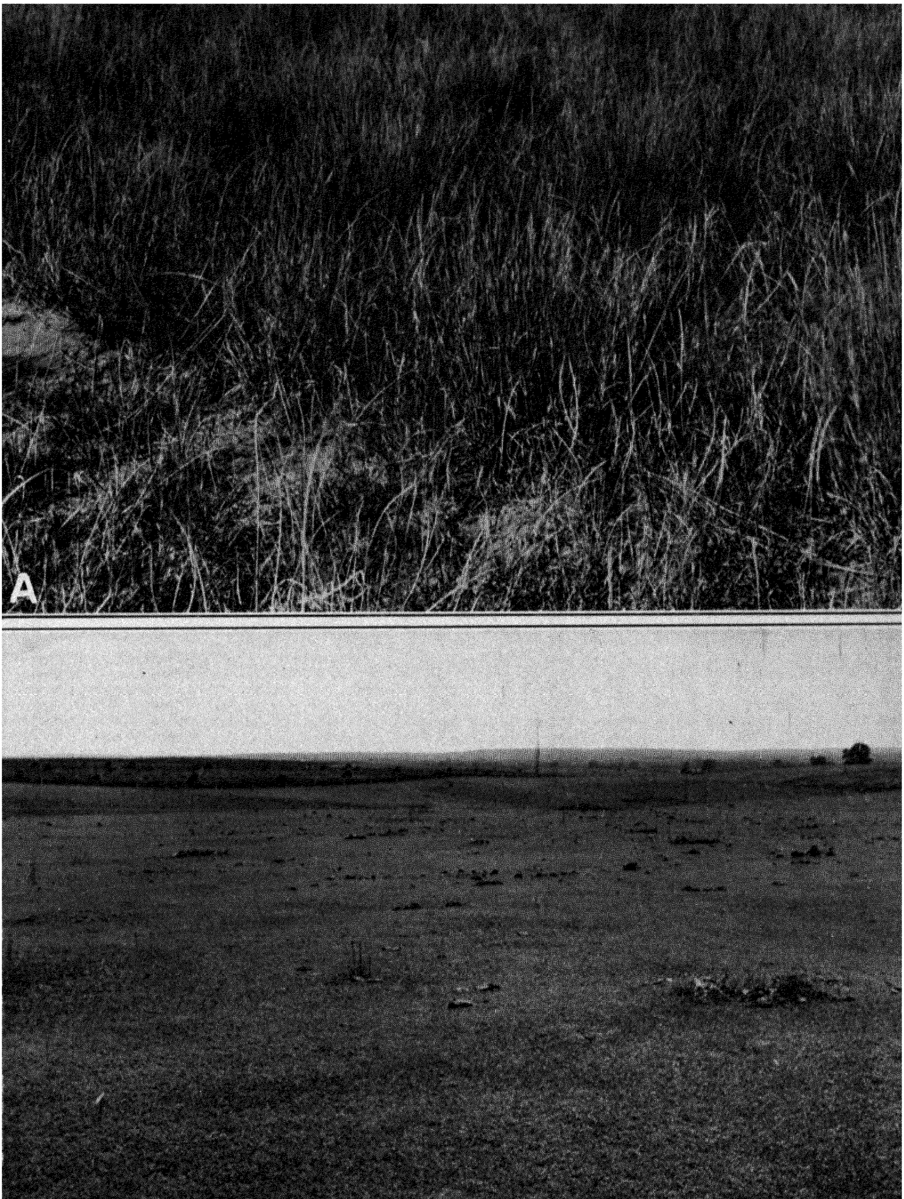
While great variations in the condition of the range can be explained by local overgrazing and subsequent recovery as a consequence of succession, further explanation can be found in the action of climatic cycles. The chief effect of the dry phase of the cycle was found in the impetus given to overgrazing, while the wet phase favored successional processes and hastened recovery. Climatic changes also serve to explain many of the contradictory statements as to the same locality. Even under ordinary conditions of grazing, the same area would be strikingly different during a drought period and the preceding or following wet phase. If it were visited at a time when drought and overgrazing coincided, and then at one in which more or less complete recovery were followed by a wet period, no greater contrast could be imagined. Moreover, while the effects of overgrazing were usually local, those of drought periods were general for the most part, and hence climatic

cycles are especially important in furnishing the explanation of the discordant statements of explorers. The effect of drought in changing the dominants of the range is illustrated by the grassland south of the Niobrara River. In 1893, this was dominated by *Aristida purpurea* and *A. basiramea* as a result of drought and overgrazing, while by 1915 the awn-grasses had been completely replaced by the mixed prairie of tall-grasses and short-grasses, which was undoubtedly the original climax.

Relations of tall-grasses and short-grasses.—The explanation of the apparent replacement of buffalo grass by the bluestems, as well as the general replacement of tall-grasses by short-grasses, has been found in the effect of grazing upon such a mixed community. This effect is naturally increased by drought periods, and it is especially in connection with such periods that the impression of a permanent change arises. Mixed prairies of tall *Andropogon* or *Stipa spartea* with short *Bulbilis* and *Bouteloua* are found in central Nebraska and Kansas, and also in the eastern Dakotas, while in western Nebraska, the Dakotas, Montana, and Wyoming they consist of *Agropyrum* or *Stipa comata* with *Bulbilis, Bouteloua,* or both of them. It is in these regions that the view has been more or less general that the tall-grasses have replaced the short-grasses as a consequence of the disappearance of the buffalo and the coming of man. This view has been held by so many keen observers, both practical and scientific, as to indicate that it has an actual foundation of fact. This has proved to be the case, but it was impossible to recognize the basic facts until the principles of succession were brought into use. A particular study of the effects of overgrazing upon mixed prairie with respect to wet and dry periods has been made since 1914. This quickly revealed the fact that the short-grasses were often completely hidden by the tall ones in times of unusual wetness, such as 1915, and that overgrazing regularly brought the tall-grasses to the point of apparently complete disappearance during drought periods. These facts have been repeatedly confirmed in adjacent grazed and ungrazed areas throughout the mixed prairie from North Dakota to Kansas, and they are regarded as furnishing a complete explanation of the apparent disappearance of the short-grasses and the invasion of the tall ones.

There is general agreement as to the damage done to the range by buffalo, as well as to the enormous number found on the prairies and plains from 1865 to 1875, when settlement was taking place most rapidly. In fact, the application of the term buffalo grass to the short-grasses is in harmony with the action of overgrazing in suppressing or destroying the tall-grasses. The westward movement of the buffalo and their decrease in numbers coincided with the incoming of settlers and the decrease of prairie fires. The immediate result was renewed growth of the tall-grasses, especially *Andropogon,* in areas where it had not been completely killed, and its invasion into others where it had disappeared. This tallies with the statement that the bluestems followed in the wake of the settlers, and drove out the buffalo grasses. The error involved in this is best illustrated by the statements of Bell (1869: 1:26, 43):

"Before we reached Salina, trees had become very scarce; but as we moved farther, the short tender buffalo grass gradually appeared—at first only here and there, but at last it abounded everywhere; and ever and anon we crossed the well-beaten path of the monarch of the plains. Doubtless no grass could



A. Mixed prairie of *Andropogon-Bouteloua racemosa* and *Bulbilis-Bouteloua gracilis*, under protection, Wilson, Kansas.

B. The same prairie in an adjoining pasture, showing its change to a pure short-grass sod, Wilson, Kansas.

bear so well the heavy tramp of thousands of buffalo continually passing over it; but it is a good thing for the land that, as settlers advance and domestic herds take the place of big game, the coarser, more vigorous, and deeper-rooted grasses destroy it and take its place. These new-comers grow with great luxuriance, yielding very fine hay; and at the same time loosening the sod, opening up the soil, and retaining the moisture in the ground."

The route followed by Bell from Manhattan to Salina, Fort Harker, and Hays was retraced in 1918 for the express purpose of determining the relations of the blue stems and buffalo grasses. Both buffalo grass and grama were found on the ridges and upper slopes about Manhattan, though they were secondary to the tall-grasses in importance. This relation continued westward to the Dakota hills about Kanopolis, where the short-grasses became more abundant, equaling the tall-grasses, and mixed or alternating with them. This general condition continued to Hays, but with the short-grasses increasing in abundance. Beyond Hays, they soon became controlling, though the rough bluffs along the streams maintained their mixed cover. Throughout the region from Kanopolis to Hays, overgrazed pastures exhibited a pure short-grass cover, while protected or less grazed areas showed a mixture of tall-grasses and short-grasses. It is clear that the short-grasses could not have been replaced by the tall ones as a consequence of settlement, and then have reentered the same areas under conditions of increasing cultivation. The obvious explanation is that while they have been associated in the mixed prairies for thousands of years, the tall-grasses were kept down by the buffalo in the zone of concentration resulting from advancing settlement. They reappeared with the going of the buffalo, and the disappearance of the buffalo grasses was nothing more than their being overtopped by the bluestems (plate 39).

Drought periods doubtless played a part in the behavior of the bluestems and buffalo grasses, as they certainly did in the mixed prairies of Nebraska and the Dakotas. In 1893 the gumbo plains north of the Niobrara River were dominated chiefly by *Bulbilis* and *Bouteloua gracilis*, as a consequence of excessive drought and overgrazing. In some places a pure cover of *Bulbilis* stretched for many miles, almost unbroken by societies. This region has been revisited several times from 1915 to 1918. The stretches of buffalo grass and grama have disappeared, and in their stead is a mixed prairie of *Andropogons*, *Agropyrum*, and *Stipa*, below which is a more or less well-developed layer of short-grasses. The drought of 1893-95 had a similar effect upon the mixed prairie of western Nebraska, in which *Stipa* was the most conspicuous dominant. This disappeared so completely, leaving a pure short-grass cover, that it was regarded as a new grass invading for the first time when it reappeared in great quantity during the rainy years of 1897-98. Williams (1898:54) has shown that dry periods have the same effect upon the appearance of *Agropyrum* in the mixed prairies of the Dakotas. It was thought that the tall-grasses might again disappear apparently during the drought period of 1916-18, but this took place only in overgrazed pastures, showing that overgrazing is an essential feature.

Overgrazing cycles.—The existence of cycles of overgrazing is beyond question, and it is possible to recognize several kinds. The simplest and shortest is brought about by such destructive overgrazing that the area will no

longer support the animals upon it. In the case of wild animals, such as the buffalo, horse, etc., the herds sought a new range, while on restricted areas the cattle died from starvation or were shipped out. In either event the grasses were given an opportunity to regenerate, or in the worst cases the processes of succession brought about a gradual return to the original conditions. Such overgrazing cycles correspond to the cycle of a subsere, and are relatively short, lasting 10 to 15 years on an average. Such cycles also occur when overgrazed or worn-out pastures are permitted to "rest." A much more important cycle is that of the double sun-spot period, namely, 22 to 23 years. This is due to the fact that overgrazing has much more serious consequences during maximum periods of drought, such as 1871-73, 1893-95, and 1916-18. The effects upon the range and the herd are much more marked than when overgrazing alone is concerned, but an enforced period of rest ensues, during which successional processes bring about the restoration of the original grass cover, unless again disturbed by overgrazing. It is this cycle which, in its beginning, has been especially disastrous to the grazing industry of the West, just as the subsequent and inevitable regeneration through succession offers the solution of all overgrazing problems. In addition, there are major cycles of overgrazing, such as are involved in the permanent migration of great herds from one region to another, or in the appearance of new species or groups of grazing animals. Some such cycle must have marked the reintroduction and spread of the horse over the plains of the Southwest. The consideration of such cycles is beyond the scope of the present treatment, and is reserved for another place.

The recognition of past and present cycles of overgrazing is of great practical importance. Its greatest value lies in the certainty that a range will return to its normal condition once it is given a chance to regenerate. It also emphasizes the fact that it usually takes several to many years to really "wear out" a range, and that the rate of recovery is roughly proportional to the length of the period of overgrazing. All the statements agree as to the excessive damage done to the range by buffalo, but it seems certain that the more or less complete rest which followed brought about a fair degree of recovery in a few years. This is not an excuse for overgrazing, since the latter always involves a distinct economic loss, the amount depending upon the period and the intensity, but it does make it clear that all overgrazed ranges can be certainly and greatly improved by proper rest or rotation. This is the basis of all range improvement, as is shown in some detail in the next section.

RANGE IMPROVEMENT.

History.—The first proposal to improve the ranges of the West by rotation grazing was made by Smith (1895:323), although suggestions for their improvement by planting cultivated species had been made by Bessey (1887, 1893, 1897), Georgeson (1895), and others. It is probable that the first suggestion as to the good effects of resting the range came from the ranchmen (Williams, 1898:72), and it is not impossible that the practice of the buffalo in leaving overgrazed regions had also led to this conclusion. In his two papers of 1895 and 1899, Smith outlined the major features of range improvement, while at the same time Williams (1897, 1898) proposed those which had to do with the artificial treatment of the range. The system advanced by

Smith comprised (1) proper stocking, (2) rotation, (3) adequate water development, (4) destruction of rodents, (5) destruction of weeds and cacti (6) disking the soil, (7) sowing and planting, (8) provision of forage, and (9) winter protection. He was also the first to organize definite grazing experiments to determine carrying capacity and the effects of rotation. The method suggested by Williams involved (1) proper stocking, (2) harrowing the soil, (3) top-dressing with stable manure, (4) sowing wild or cultivated forage plants, (5) keeping weeds mowed, (6) water development, (7) rest. Since the work of these two pioneers in range improvement, the subject has been discussed more or less completely or from various sides by Bentley (1898, 1902), Nelson (1898), Shear (1901), Griffiths (1901, 1902, 1903, 1904, 1907, 1910), Davy (1902), Cotton (1905, 1908), Wooton (1908, 1915, 1916), Sampson (1908, 1909, 1913, 1914, 1918, 1919), Jardine (1908, 1911, 1912), Thornber (1910, 1914), Wilcox (1911), Barnes (1913), Darlington (1915), Barnes and Jardine (1916), Potter (1917), Jardine and Hurtt (1917), Clements (1917, 1918, 1919), Sarvis (1919), and Jardine and Anderson (1919).

The first experimental study of grazing was carried on at Abilene and Channing, Texas, from 1899 to 1901 by Smith and Bentley (p. 226). Experiments under practical grazing conditions have been made on the Jornada and Santa Rita Range Reserves of the Forest Service for the past seven years. Intensive studies in smaller pastures and hence under closer control have been carried on by the Office of Dry-Land Agriculture at Mandan, North Dakota, since 1915, and at Ardmore, South Dakota, since 1918. Both the field and experimental studies have conclusively demonstrated the essentials of range improvement and have made it possible to outline a complete system based upon investigation as well as practice.

Prerequisites.—In addition to the actual processes concerned in improving the range, certain factors are prerequisite to any improvement or necessary for the best results. By far the most important of these is adequate control, without which improvement is all but impossible. It is immaterial whether control is secured through ownership or leasing, provided it permits fencing. However, leasing has the indirect advantage that it enables the State to exact certain conditions as to utilization. The value of control in preventing overstocking and permitting rotation is obvious. Next in importance is a practical appreciation of the inevitable recurrence of dry and wet periods and their critical effect upon the range. It is imperative that the ranchman be prepared to reduce the pressure upon his range as the dry phase of the climatic cycle approaches and that he be ready to take full advantage of the excess carrying capacity of the wet phase. In fact, the whole system of improvement must be focussed upon the destructive effect of overgrazing in dry years and the possibility of greater utilization and of successful sowing and planting during wet years. Furthermore, there must be some recognition of the universal processes of succession and their importance in regeneration. It is necessary to take into full account the fact that destructive overgrazing, trampling, and other disturbances will destroy the grass communities and make place for one of weeds. Even more important is the recognition of the fact that weed communities will be maintained indefinitely by continued overgrazing or disturbance, or that they will slowly give way to the returning grasses if the area is protected for a time. In short, an elementary under-

standing of successional processes furnishes a tool for manipulating the grazing cover more or less as desired. Finally, a trustworthy idea of the condition and tendency of the range is impossible without adequate methods of measurement. In practice, such methods can best be supplied by indicator plants, and by a careful check upon the condition of animals when they enter and leave the range. In both investigation and demonstration, however, more accurate measurements are necessary, especially in connection with the varying carrying capacity of wet and dry periods. Changes in composition and variations in production year by year can be determined only by the use of permanent quadrats. Some of these are charted, while others are clipped and the herbage weighed. The most significant measurement, however, is that furnished by weighing the individual animals from month to month, or at the beginning and end of the season.

Essential factors.—Range improvement may be effected in some degree by any one of a large number of processes. Thoroughgoing improvement, however, must take them all into account, is so far as they are concerned in a particular range. It is obvious that some of these, such as proper stocking and rotation grazing, are of universal importance, while others, such as the eradication of prairie-dogs or poisonous plants, apply to certain ranges. The essential features of the complete system of range improvement proposed here are: (1) proper stocking; (2) rotation or deferred grazing; (3) eradication of rodents, poisonous plants, weeds, etc.; (4) manipulation of the range by clearing, burning, etc.; (5) improving the cover by sowing and planting; (6) forage development; (7) water development; (8) herd management. Contributing factors are found in classification and range surveys, the economic aspects of ranch management, and an adequate land system. Practically all of these have been regarded as more or less essential to range improvement since the first proposal of Smith, 25 years ago, and the present treatment assumes only to correlate them more closely and to work some of them out in greater detail. The distinctive features of the system are the use of climatic cycles and succession as universal bases, the employment of indicator plants, the use of enclosures and exclosures together with permanent quadrats as measures, and the development of new methods of manipulating and modifying the range, especially in the production of mixed grazing types.

Proper stocking.—The primary object of range improvement is to secure and maintain the maximum carrying capacity. The chief factors in this are proper stocking and rotation grazing. The optimum degree of stocking, however, can be determined only by actual trial accompanied by measurement of the results. Such trials can be made by the ranchman himself wherever he has control of his range, but until their necessity becomes generally recognized they must be made for the different grazing types by the experiment stations and similar agencies. The investigation of carrying capacity by actual grazing test can be made by either the extensive or intensive method. The first is more practical on ranges as they exist; the latter is more accurate and demands a greater equipment. The results of an extensive study of carrying capacity on the Jornada Reserve have been brought togther by Jardine and Hurtt (1917:12). Eight different grazing types occur on the reserve and the carrying capacity varies greatly for the different communities. Permanent quadrats were employed to determine variations in yield from year

to year, as well as the rate of increase under rotation or protection. Since both rotation and reserve grazing were necessarily practiced, no definite studies were made of the basic carrying capacity under full grazing for the entire season. Such studies are possible only under the intensive method and in an essentially uniform type. Their great value lies in making it possible to check the assumed optimum carrying capacity by rates of grazing which reveal both over- and under-utilization, and in demonstrating the additional gain resulting from rotation methods. Installations for the intensive study of carrying capacity and rotation grazing have been made by the Office of Dry-Land Agriculture at Mandan and at Ardmore. Both are located in the mixed prairie, the one in *Stipa-Bouteloua*, and the other in *Bulbilis-Agropyrum-Bouteloua*. Since the methods are essentially alike, it will suffice to describe briefly the experiments at Mandan, which have been under way since 1915.

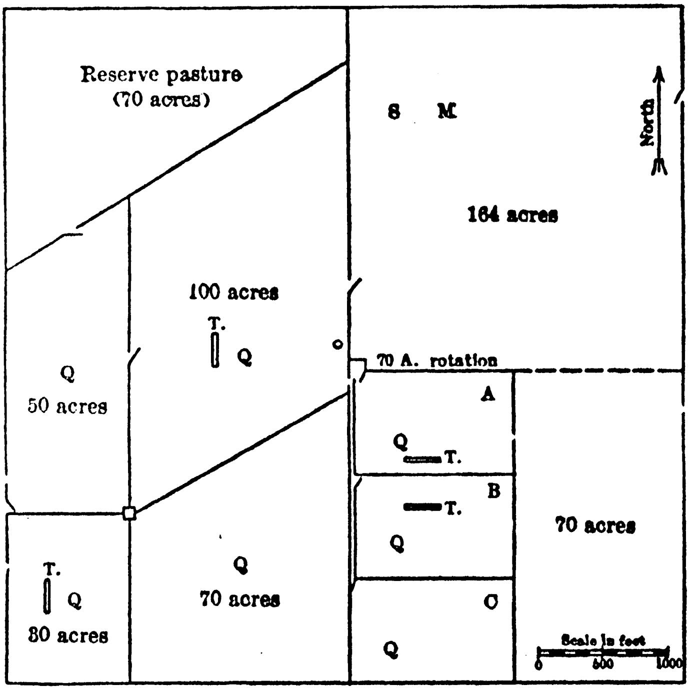


FIG. 21.—Pastures for the intensive study of carrying capacity and rotation grazing, Mandan, North Dakota. After Sarvis.

There are four pastures for the investigation of carrying capacity under continuous grazing, two for rotation grazing, a reserve pasture, and one for the study of hay development (fig. 21). At Ardmore two pastures are devoted to continuous grazing and the same number to rotation. The four pastures contain respectively 30, 50, 70, and 100 acres. Since each pasture is grazed by 10 two-year-old steers, the corresponding rates of grazing are 1:3, 1:5, 1:7, and 1:10. Each pasture contains an exclosure termed an isolation transect (fig. 22), which is 300 feet long and 60 feet wide. This consists of three strips, of which the central one, *P*, serves as permanent transect

for annual comparison with the grazing and regeneration transects on either side, as well as for the installation of permanent quadrats of various types. One unit of the grazing transect, *G*, is unfenced for each year of the climatic cycle, while one of the regeneration transect, *R*, is fenced for each successive year of the cycle. The central position of the permanent transect permits ready comparison between the protected area and those fenced and unfenced for each successive year, as well as actual measurement in all three areas by means of chart and clip quadrats. Similar quadrats are located in the open pasture, thus completing the measurement of all areas year by year. It is evident that the grazed transect will also show in series the effects of unfencing for 14, 13, etc., years down to 1, and that the regeneration transect will show those of fencing for a similar series of years. Finally, special quadrats are located in the transect to reveal the effects of burning or clipping at various times and intervals.

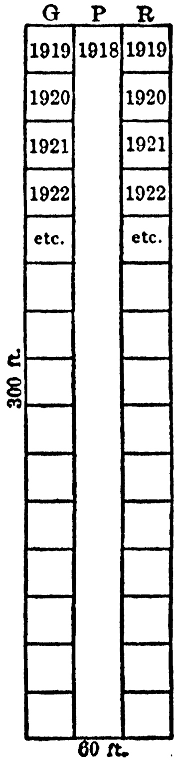
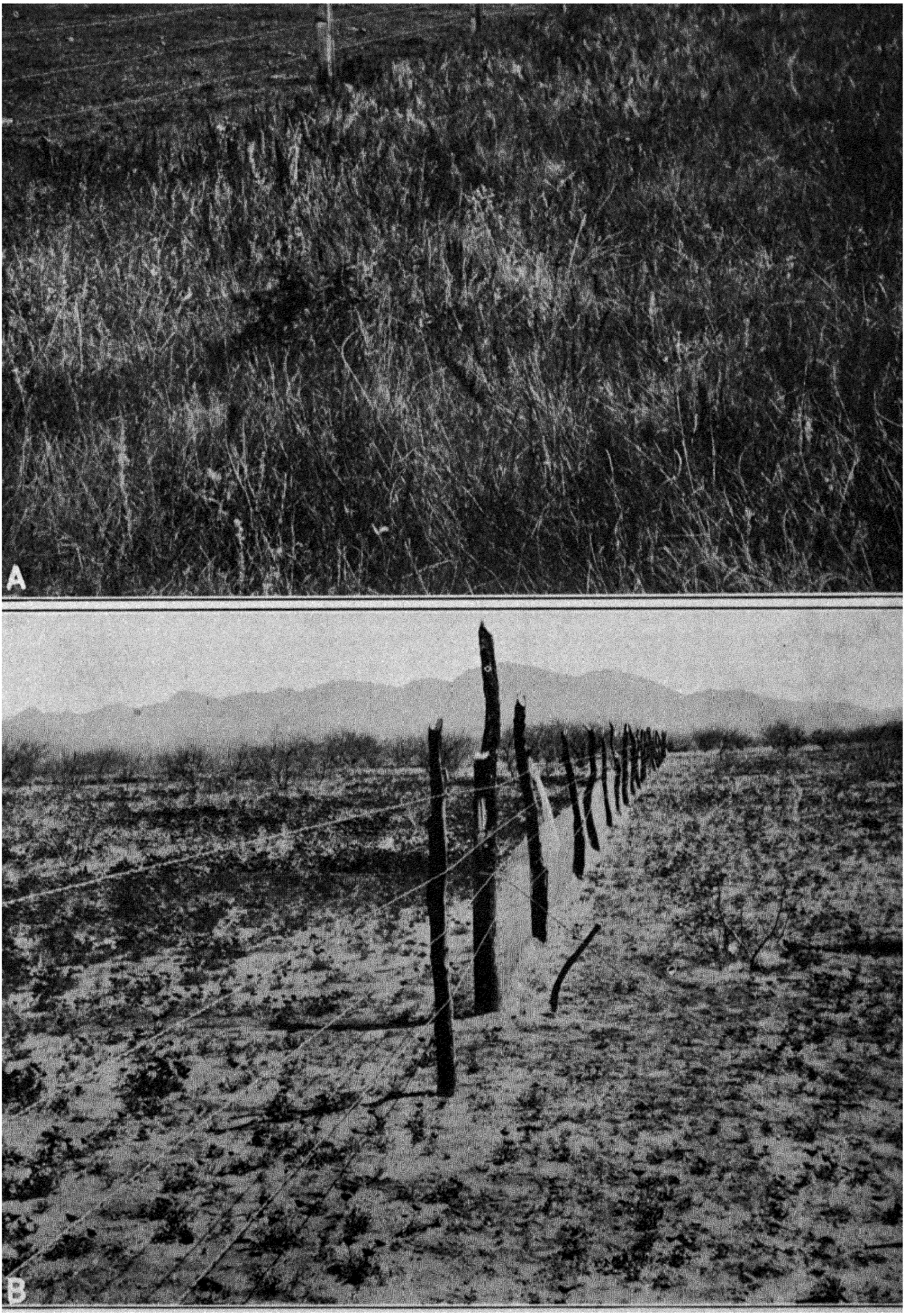


Fig. 22.—Isolation transect for measuring cyclic changes in yield under protection and under grazing.

With reference to the cattle to be used, it is necessary that they be of the same breed, age, and class, and in as nearly the same condition as possible. It will probably prove desirable to determine the carrying capacity of the same grazing type for different species, as well as for different breeds, etc., but this will require pastures of the same size and involves an expansion of the work which is unnecessary at present. The cattle are weighed at the beginning and end of the grazing season and at monthly intervals during it. This is accomplished by means of four corrals, one for each pasture, leading to the scales for weighing (fig. 23). A special method of management has been developed for handling the cattle in the pastures and at the times of weighing, the main details of which have been given by Sarvis (1919). The detailed results of the experiment have not yet been published, but the evidence furnished by the various pastures, in terms of cover and indicator plants, has been most striking (plate 40, A), and these have been verified by the behavior and weights of the different herds.

Rotation grazing.—First suggested by Smith in 1895 and begun experimentally by him and Bentley in 1899, rotation grazing has been developed chiefly by the Forest Service since 1910. The scientific basis for deferred and rotation grazing was largely developed by Sampson (1908, 1909, 1913), and it has been applied to actual grazing on the national forests. It has had its most thorough demonstration on the Jornada and Santa Rita Range Reserves, but especially on the former. Pastures for the study of rotation were installed at the Mandan and Ardmore stations in 1918, but conclusive results can not be expected for several years. Rotation grazing is an inclusive term which is regarded as applying to all methods of alternate grazing and rest, partial or complete. Deferred grazing is the type in which the pasture is completely protected or only lightly grazed during critical periods in the life-history of the chief dominants. This is usually the period of seed-production, but on



A. Isolation transect in *Stipa-Bouteloua* pasture, Mandan, North Dakota.
B. Grazing exclosure with cattle-proof and rodent-proof units; crop of winter annuals, chiefly *Eschscholtzia mexicana*; Santa Rita Reserve, Tucson, Arizona.

certain types it may fall at the opening of the growing season. Reserve grazing is that in which a pasture is kept in reserve for emergencies, especially those due to drought, or where the grazing during the season, though uniform, is sufficiently light to permit a fair amount of seed to be produced.

The classic experiment in rotation grazing is that carried on by the Forest Service in cooperation with Mr. C. P. Turney on the Jornada Reserve near Las Cruces, New Mexico. This has been described in detail by Jardine and Hurtt (1917:28), and their conclusions as to range improvement by natural revegetation are given here:

"Primarily as a result of (1) reducing the number of stock during the main growing season of about four months—July to October—to about half of the average number the area will carry for the year, (2) not overstocking during the other eight months, and (3) better distribution of stock watering places, grama-grass range on the Jornada Range Reserve has improved in three years at least 50 per cent as compared with similar adjoining unfenced range grazed yearlong.

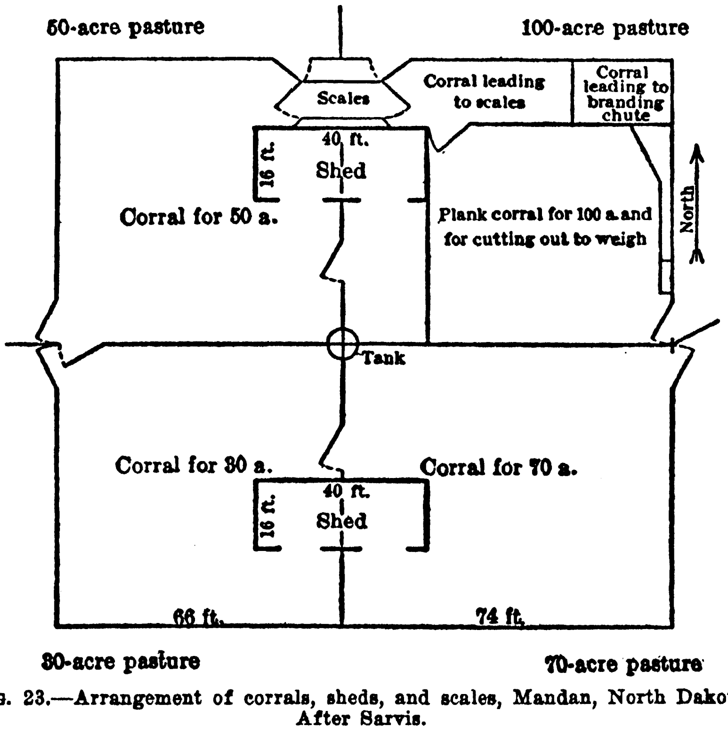


FIG. 23.—Arrangement of corrals, sheds, and scales, Mandan, North Dakota. After Sarvis.

"On fenced grama-grass ranges of the Southwest where the stock are carried mainly on range feed throughout the year, light stocking during the growing season is profitable. It will probably not reduce the total animal-days feed furnished on a given area during the year, and will reserve feed for the critical period from February to July, and later in case of prolonged drought.

"Where the whole of a range unit is made up of grama or similar grass, about one-third of the area should probably be reserved for light grazing

during the growing season two years in succession. Each third in turn should be given as nearly as practicable this amount of protection. By light grazing is meant grazing by not more than half the average number of stock that the area will carry for the year as a whole."

Rodent eradication.—Smith (1899:15) was apparently the first to emphasize the damage done by rodents to the range and to urge the systematic extermination of prairie-dogs and jack-rabbits. While much has been said and written on the control and extermination of prairie-dogs in particular since 1900, effective campaigns against these and other rodents are recent developments. During the last five years especially, the Biological Survey has carried on systematic and effective work in the eradication of both prairie-dogs and ground-squirrels, in cooperation with various States, as well as with the Forest Service and with private individuals (Bell, 1917; Lantz, 1918). In addition, California has organized an extensive campaign through its Rodent Control Section. It has also come to be recognized that jack-rabbits are often exceedingly destructive to the range, and the work of Vorhies (1919) has shown that the kangaroo-rats of the Southwest must also be included among the major pests. While various methods have been used to exterminate or control rodents, that of poisoning has become the standard, because of its economy and efficiency. However, it has become clear that complete eradication is possible only through poisoning for two or three successive seasons, and that re-immigration can be controlled only by dealing with large and more or less natural areas and by the extermination of invading colonies from time to time.

The absence of accurate knowledge as to the amount and kind of damage done to the range by rodents, and especially of the rate and degree of recovery in various types after eradication, led the writer to suggest the desirability of cooperative studies to the Biological Survey, the Forest Service, and the University of Arizona. As a consequence, fenced areas for such investigations were established in 1918 in the *Bouteloua-Aristida* grassland of the Santa Rita range reserve and in the *Bouteloua gracilis* subclimax of northern Arizona near Seligmann and Williams. The latter were designed to study the recovery after the eradication of prairie-dogs, while the former were to permit a more intensive study with reference to jack-rabbits, and specially kangaroo-rats, which had just been shown by Vorhies to cause even more serious damage. A series of three exclosures was installed in the *Bouteloua rothrockii-Aristida californica* type of the reserve (plate 40, B). The first was fenced against both rodents and cattle, and the second and third against cattle alone, but differing in that the rodents were killed out of one. A second exclosure was established in the *Bouteloua eriopoda-Aristida divaricata* type, which was also fenced against rodents and cattle. For the sake of a direct determination of the amount of forage consumed by jack-rabbits and kangaroo-rats, two inclosures were located in one of the best areas of *Bouteloua rothrockii.* In one of these were placed two rabbits, in the other two kangaroo-rats. Permanent quadrats were located for measuring the effects in the various inclosures as well as in the pastures by means of charting and clipping. The critically dry summer of 1918 almost completely prevented the growth of grass and summer annuals, and practically all quadrats contained less growth in the fall than in the spring. The winter rains were nearly normal and so well distributed that

the growth of winter annuals was exceptional. As a consequence, the various fenced areas showed striking improvement in total production over the pastures. This was not only true of the cattle-proof exclosures, but of the rodent ones likewise, proving that the rodents also take heavy toll from the winter annuals as well.

Special studies were made of the life history and food habits of the kangaroo-rat in particular, and the latter was found to have a decisive bearing upon the dominance of the grasses (Vorhies, 1919). Burrows excavated in the winter of 1917-18 showed that the kangaroo-rat stored large amounts of food and that this consisted chiefly of the spikes of *Bouteloua.* Those excavated in 1918-19 exhibited no grass spikes, owing to their failure to form during the drought of the preceding summer, but the bulk of the stored food consisted of the crowns of *Bouteloua rothrockii.* When the size of the denuded area about each burrow is taken into account, it is readily seen that the damage done by kangaroo-rats is exceedingly serious, especially in periods of drought. While they occur throughout the desert scrub, it seems probable that the majority have migrated upwards into the desert plains as the grasses were eaten off at the lower levels. The persistence of the grasses in sheltered spots and their reappearance in fenced areas in the desert scrub suggests that they can be successfully reintroduced into the deserts about Tucson after the kangaroo-rats have been exterminated. The rats which persist in the desert now live in part upon the shrubs, it seems, and in consequence the latter are now being killed out over great stretches from Ajo to Yuma and beyond.

In addition to the major pests, the pocket-gopher, wood-rat or pack-rat, and several of the field mice do more or less damage to the range. The gopher damages the range by eating grass roots and disturbing the soil with his burrows, but the injury is usually restricted to small areas. The pack-rat lives on leaves of *Yucca* by preference, especially *Y. radiosa* and *Y. arborescens,* and may do considerable damage in regions where these are important supplementary forage. In the desert scrub and plains, it seems to feed largely upon various species of *Opuntia,* which are heaped up about its nest.

Eradication of poisonous plants.—The loss of range stock from eating poisonous plants is so evident and often so serious that the importance of its prevention requires no argument. The chief difficulty in the way lies in the general ignorance of poisonous species and of the best methods of dealing with them. Quite apart from their poisonous properties, such species are usually undesirable weeds which compete successfully with the grasses and thus reduce the carrying capacity of the range. As a consequence, eradication is theoretically the most satisfactory way of dealing with them, but this is perhaps economically possible only in small pastures and other local areas. Where they grow over hundreds of square miles, as in the case of the loco-weed, *Aragalus lamberti,* on the plains and foothills along the eastern front of the Rocky Mountains, eradication is practically impossible under existing conditions, and controlled grazing is the only practicable method of prevention. Marsh (1918:21) has stated:

"Most of the losses from poisonous plants occur at times when the animals are short of feed and the larger part of the stock poisoning is indirectly due to scarcity of proper forage. This fact of the intimate relation of scarcity of feed to stock poisoning can not be too strongly impressed upon the people

who handle range animals in the West. There is apparently a popular idea that range animals will voluntarily seek out poisonous plants and eat them by preference. It may be stated as a general fact that this is not true. Animals seldom eat poisonous plants except as they are driven to do so by the lack of other food. Almost all poisonous plants are actually distasteful to live-stock and under ordinary circumstances will be avoided. The only exception to this, perhaps, is the group of loco plants. Animals do frequently acquire a taste for loco and under some circumstances will eat nothing else, even in the presence of other forage; and yet the initial feeding in the case of loco plants is almost invariably brought about by the scarcity of food.

"It has long been known that loco eating is ordinarily commenced in the winter season or in the early spring, when the loco plants are green and luscious and before the grass has started. The loco plants at that time are the most prominent plants on the plains and animals commence to eat them because of lack of other food. In the matter of other plants, the relation between starvation and the eating of the poisonous plant is still more marked. For instance, the larkspurs spring up immediately after the snow leaves the mountains and grow much more rapidly than the surrounding grasses, and if cattle are allowed to go up to the upper ranges before the grasses have had a fair start they find already occupying the ground the succulent larkspur plants in large numbers. Sometimes the cattle come from dry winter feed and are anxious to gorge themselves with any green material they find. Under such circumstances, if they come upon a field of larkspur they frequently eat enough to produce fatal consequences. Later in the season there is very much less danger from larkspur because of the abundance of other food. If, however, cattle are driven from one range to another and the trail passes through a mass of tall larkspur, it is not at all unusual for the hungry animals to grab hastily at the plants and this may result in disastrous consequences. Under such circumstances it is important that the cattle shall not be driven rapidly, for they will snatch all the more, and they should also have been thoroughly fed before going on such a drive.

"It is also evident from what has been said earlier in this paper, that if cattle can be kept off fields of larkspur until after the plant has blossomed, little trouble may be expected. This method has been employed for many years in Colorado, where it is a common practice to "ride for poison," as it is called; that is, the herders ride and keep the cattle down from the higher ranges until the larkspur has blossoned and matured, after which there is no further danger. The same thing has been accomplished in certain regions by putting up drift fences which are designed to keep the cattle on the lower ranges until the danger is past. There are valleys known as death traps for cattle. Frequently it will be found that in these valleys the tall larkspur is thriving in large clumps and cattle drifting in will feed freely upon it. It is often possible, under such conditions, to clear out this larkspur or enough of it so there will be no danger. In order to kill the plants the roots of most species should be cut off at least 6 or 8 inches below the surface.

"The losses of sheep from death camas (*Zygadenus*) occur under very similar conditions to those of cattle from larkspur. *Zygadenus* grows very early in the spring. It precedes the grasses in its growth and is present in a succulent condition at a time when other forage is extremely scarce. Inasmuch as it occurs frequently in large masses, if sheep are trailed over these places they are liable to get enough to cause heavy losses. It is particularly important in the handling of sheep in such localities that, if possible, they be grazed in loose order. When the animals are massed together, they will eat

everything in their course, and because of jealousy will take particular pains to get every available plant.

"This applies equally well to lupine poisoning. When sheep are allowed to feed freely upon a lupine patch and are moved without haste, no harmful results will occur. If, however, they are massed together and driven in close formation over such a patch, they are almost certain to be poisoned if the plants are in pod at the time. The remedy in such cases clearly is to see that the sheep, when it is necessary to trail them through a patch of lupine, are drifted rather than driven, and that they are well fed when they come upon this locality. It seems probable that intelligent handling of bands of sheep may reduce to almost nothing the losses occasioned by *Zygadenus* and lupine. If, however, hungry sheep come in contact with fields of *Zygadenus* in the spring or with fields of lupine in the late summer and fall, at a time when the plants are bearing pods, fatal results must be expected."

Poisonous plants can be eradicated or kept down to a point where they are not dangerous in various ways. The most thorough and likewise the most expensive is that of grubbing out the roots. At the Utah Experiment Station of the Forest Service, Sampson has found that cutting or mowing two or three times during the first growing season and once or twice the second prevents storage in the rootstocks and leads to the dying-out of the plants. Where the ground is not too uneven or covered with brush, it is much cheaper than grubbing, and nearly as efficacious. Sheep have also been used to graze off larkspur on cattle ranges, and it appears probable that overplanting with vigorous innocuous species during favorable seasons would largely eliminate poisonous plants as a result of competition.

Aldous (1917:22) has summarized the results of the methods of grubbing out and grazing off larkspur on the national forests:

"Grubbing out the plants is the most feasible method of preventing loss of cattle from tall larkspur poisoning. The first grubbing costs from $3.65 to $10.10 per acre, the cost depending upon (1) the number of plants per acre, (2) the texture of the soil, and (3) whether or not the plants are growing in the open or in willows or other brush. The cost of the second grubbing should not exceed $1 per acre. Extensive eradication on four forests has been done at a cost of less than one-half the value of the cattle saved annually. An average of 93 per cent of the plants in the experimental work and of from 80 to 95 per cent in extensive work were killed by the first grubbing. By a regrubbing of the area one year after the first grubbing practically all of the larkspur plants were killed.

"The use of sheep to graze off larkspur-infested cattle range has a limited application. Its success depends (1) on the palatability of the larkspur, (2) the availability of sheep to graze the infested area at the proper time, and (3) whether the infested areas furnish sufficient forage to justify trailing sheep to them."

On the lower ranges, especially those of the grassland climax, overgrazing is either a direct or a contributing cause of stock poisoning. This is naturally the consequence of the disappearance of the more palatable species and the correspondingly greater abundance and attractiveness of the poisonous weeds. Since the evil effects of overgrazing are most in evidence during the dry phase of the climatic cycle, methods of control and eradication should be focussed especially upon drought periods. For example, the grubbing out of plains

larkspur or loco would be a simpler matter at the end of a drought period, and the grasses would be enabled to develop a much more effective competition during the ensuing wet period.

Eradication of weeds and cacti.—It has been repeatedly shown that annual herbs are replaced in the course of succession by perennial ones, and these to a large degree by grasses. The weedy nature of the annuals is evident, but perennials are often also to be regarded as weeds in a grass range, especially one used by cattle or horses. Under climax conditions, the grasses are able to maintain their dominance in competition with the herbs, but in the case of overgrazing or other disturbance, the latter gradually get the upper hand. When the area is protected or the grazing reduced, the advantages of the grass life-form again come into play in the competition, and the herbs disappear or become subdominant. As a consequence, the best method of eradicating weeds is by protection or regulated grazing. Complete protection is more rapid in its effects, but it is usually out of the question. Regulated grazing is the most practicable method as a general rule, but it is sometimes too slow in operation, or the area is too thoroughly dominated by weeds to permit it. This is particularly the case with areas densely covered with prostrate species of prickly pears, such as *Opuntia mesacantha* and *O. polyacantha*, or with half-shrubs, such as *Gutierrezia*.

When it is desired to get rid of annual weeds more rapidly than by means of regulated grazing, they may be grazed off by sheep, especially where mixed grazing is practiced. They may be greatly reduced by burning at the time when their seeds are ripening, and they may even be mowed where the area permits. During favorable seasons, their disappearance may be hastened by overplanting with more vigorous species, especially perennials, which increase the natural rate of succession. Perennial weeds are more difficult to get rid of, since they are less affected by burning or mowing, and it is too expensive to grub them out on the range as a rule. Fortunately, the most serious pests are cacti and half-shrubs, which lend themselves to various methods of clearing. Since cacti furnish succulent forage when more or less spineless, the most satisfactory method of eradication is by burning, when the tract contains enough grass to permit this, or by singeing with a torch when the area is almost pure. Once the spines are removed from the prickly pears, they will be grazed down to the ground by cattle, and in a few years will practically disappear from the range if overgrazing is prevented. Halfshrubs, like other weeds, can best be eliminated by protecting the areas or grazing them lightly, but many ranges are so densely covered with *Gutierrezia* or *Isocoma*, for example, that other methods must be employed. Since these rarely root-sprout, burning is the quickest and most economical method, though in small areas they may be cut out with profit.

Eradication of brush.—The range value of brush is determined primarily by its palatability, but it depends in a large measure also upon whether it is pure or mixed with grass. As has already been emphasized, a range made up of grass and browse in more or less equal degree permits mixed grazing and furnishes the best insurance against drought and other disasters. The burning of unpalatable brush to clear the ground for herbaceous growth seems to have been long practiced in California, and it has also been employed to maintain the stand of grass against the encroachments of shrubs in mixed

types. In the case of the Coastal chaparral, the dominants form root-sprouts in great abundance and repeated burning is necessary to maintain the herb cover. This is less true as a rule in the Petran type, where burning is chiefly important in enlarging the grass areas, as is the case likewise in the subclimax chaparral of Texas. In the typical savannah of the Southwest, the mesquite and its associates may be kept down by burning and the grassland climax favored. In the case of sagebrush, grazing by cattle favors the shrubs at the expense of the grasses, and the latter can be maintained only by some practice which handicaps the brush. Since *Artemisia* and its associates usually form few root-sprouts, fire furnishes the simplest way of restoring the balance from time to time. Clearing is even more effective, but out of the question because of the expense. Sagebrush may also be driven out by the grasses where irrigation or flooding occurs, but this is rarely feasible in range practice.

Manipulation of the range.—Fire is but one of several processes which may be used to bring about modifications of the forage cover. In addition to the similar process of clearing are (1) cultivating, (2) irrigating, (3) fertilizing, (4) cutting and pruning, and (5) sowing and planting. Besides its use in handicapping scrub in mixed types, fire is of especial value in destroying the old stems of bluestems and bunch-grasses, and making the new growth available for grazing. Throughout the grassland climax from Canada to Mexico occur frequent and extensive areas of *Andropogon* which are utilized little or not at all, except when hunger drives the cattle to graze them during drought years. However, when the dead stems are burned in the winter or early spring, the new growth is readily eaten, and with proper management the bluestems and similar coarse grasses can be kept in constant commission in the grazing practice. There is still a wide difference of opinion as to the ordinary effect of fire upon grassland, and this is one of the many grazing problems which need exact investigation in various types. Theoretically the burning of prairie every few years should constitute a desirable practice, if the year and season are chosen in such a way as to avoid injury to the underground parts. In the short-grass and desert plains, fire would probably always do more harm than good, owing to the dry soil and the certainty of injuring the roots and rootstocks. Annual fires in grassland are probably always harmful, especially in regions where less desirable annual species are present. Fire has undoubtedly played a large part in the spread of *Bromus tectorum* and related species, as well as of *Avena fatua*, and it now is largely responsible for maintaining them against the perennials. However, in the regions where *Avena* is a desirable range or hay grass, fire is of value, since this annual would slowly yield to other dominants if fire and other disturbing agents were removed. Apart from farming operations, clearing is practicable only in the case of particular species and over limited areas, as has already been noted for poisonous plants. In such cases, grubbing, cutting, and mowing are all modifications of clearing, which are of restricted application. In the case of browse plants, however, cutting and pruning offer means of increasing the amount of fresh browse, as well as its accessibility. These again are methods for small areas, but they promise to have real value in the case of such shrubs as the salt bushes, oaks, mesquites, catclaws, etc.

The improvement of the range by the use of some of the methods of cultivation has been tried from time to time. The first experiments in the appli-

cation of surface tillage to the range were those of Smith (1899:20) and Bentley (1901:18), which led to the conclusion that it would be profitable to cultivate pastures with disk and iron-tooth harrows, especially in the semi-arid regions. While the practice of stirring the surface soil and loosening up the root-bound sod has been frequently recommended (Georgeson, 1895:43; Williams, 1897; cf. Thornber, 1910:324), it has never been adopted for many reasons, chief among them the labor and expense involved and the great difficulty of applying intensive methods to large areas. This is equally true of the application of fertilizers to increase the growth of grasses, and of the use of irrigation. The application of manure to worn-out pastures was a logical extension of good farm practice, and there is little question that the composition as well as the yield of native and artificial pastures can be varied more or less at will by the scientific manipulation of different fertilizers (Skinner and Noll, 1919). However, such methods are limited to pastures in which intensive yields are possible, and are not applicable as yet to even the smaller pastures of climax grassland. Irrigation has a somewhat broader application to western ranges, because the lack of water is the chief limiting factor to production. The cost of irrigation, however, is regularly too great to permit its use, except in restricted areas, where an exceptional production can be obtained. Even in the majority of such cases, the forage is worth more as hay, and is handled in that form.

Plant introduction on the range.—The sowing or planting of desirable native or cultivated species on the range has universally been suggested and often attempted. One of the earliest trials was that of Georgeson (1895:43), who sowed a mixture of perennial grasses, clover, and bluegrass in the prairie near Manhattan, Kansas. The tame grass made a splendid growth early in the season, but by autumn it had everywhere yielded to the native dominants. Bentley (1901:16, 30) made extensive tests of native grasses when sown or transplanted in the native cover. Transplanting gave much the best results, practically all the native dominants establishing themselves successfully when due care was taken as to the time and method of transplanting. The most extensive series of experiments in seeding native grassland have been carried on in the Southwest by Griffiths, Thornber, and Wooton between 1900 and 1915. As this is the most trying region for the introduction of new plants, it affords the best idea of the difficulties involved. Griffiths has summarized the results of seeding operations on the range reserves near Tucson, as follows:

"Experimental work carried on thus far in attempting to introduce perennial forage plants upon the mesas has given very little encouragement. *Panicum texanum*, an annual, has given the best results of anything thus far introduced, and it is believed that more success will be secured with annuals than with perennials. They are not as good feed, but short-lived plants with good seed-habits now furnish the main feed upon the mesas (1904:61).

"Many attempts have been made to introduce forage plants in this section, both in the large enclosure and upon the holdings of private individuals. There is but one species, alfilerilla (*Erodium cicutarium*), that has given any beneficial results. In all, 200 species of forage plants have been tried in this enclosure. Many native species were tried, but the vast majority used were of foreign introduction. At one time the Office of Forage-Plant Investigation of the Bureau of Plant Industry furnished more than 100 varieties for testing. In some cases the seed was covered and in others scattered without any further

attention. The plan has been, whenever the quantity of seed permitted, to sow one-half in the fall and one-half in the early summer. In some cases the ground was worked up sufficiently to kill about half of the original vegetation. The net economic result of all this foreign introduction has been practically nil. Most of the species in our experience have never come up, and the few things that did make any growth usually died before seed was produced.

"A number of native grasses have been caused to spread successfully by gathering the seed in advantageous localities and simply scattering it where the ground was badly denuded. Better results have been obtained when seeding was done the last of June or the first of July. When sown in autumn the ants pick up too many of the seeds. Beneficial results have been secured in this way by the use of the seed of *Andropogon saccharoides, Bouteloua vestita*, and *B. rothrockii*. Less positive results have been secured by the use of native seed of *Bouteloua curtipendula* and *Leptochloa dubia*. Indifferent results have been secured with *Bouteloua oligostachya*. The above illustrations of the successful use of native species are important and interesting, but they have no applicability to open-range conditions. However, where the land is under fence, and seed can be secured in the vicinity without too much expense, improvements can be made in very badly trampled areas. When the roots of the native growth are not completely destroyed, it is questionable whether in such situations as this, recuperation would not occur fully as rapidly by proper protection from overgrazing without the use of seeds as with it." (1910:12.)

Thornber (1910:312) has furnished a detailed and comprehensive account of seeding and planting operations in connection with the small range reserve near Tucson:

"The almost complete failure of the above experiments in a reasonably favorable year led the writer to undertake a series of experiments on similar land receiving more water than the annual rainfall. To this end the storm water embankments or dams already noted were built and the small areas over which their flood waters occasionally extended were cultivated and sown from time to time with the more promising of the native grasses, saltbushes, and other forage plants, in addition to a number of introduced ones. For purposes of comparison, most of these varieties were sown on adjacent areas not so flooded, and also in the forage garden on the University grounds where moderate irrigation was given.

"Good stands of blue grama (*Bouteloua gracilis*), hairy grama (*B. hirsuta*), and side-oats grama (*B. racemosa*) were secured with heavy summer rainfall in addition to flooding, on the small range enclosure. These, however, gradually died out with average summer rains and little or no flooding from storm water. Crowfoot or mesa grama (*B. rothrockii*), though more or less common on the lower mesas, killed out badly with prolonged droughts. With moderate irrigation practically all the grama grasses did well in the forage garden, while without such irrigation their growth was short and they showed signs of dying out. It is quite evident therefore that the rainfall at the lower altitudes is too limited for the successful growth of these species. Silver-top or feather bluestem (*Andropogon saccharoides*) has become established whereever sown on areas subject to annual flooding, after which with average rainfall it has yielded at the rate of three-fourths to one ton of hay to the acre. It has resisted in a remarkable degree prolonged drought, never having suffered any injury therefrom when once established, and is gradually spreading over cultivated areas, and swales and mesa depressions. When sown on

the higher creosote land not subject to flooding, or during seasons with less rainfall than the average, it has failed. Tangle head (*Heteropogon contortus*) has also made a good showing on the small range enclosure, while in the forage garden it has yielded even more heavily than silver top. The sacaton grasses made little or no growth from the start with rainfall heavier than the average on land not flooded, and this was true of a number of other grasses, including *Hilaria, Stipa,* and *Aristida.*

"No introduced forage plants, including species from cool, moist climates and higher altitudes, made any growth on the small range enclosure, and but few of them persisted in the forage garden for any considerable length of time. Both the native and Australian saltbushes failed repeatedly to secure a hold or make any growth of extended duration, though they were planted on land occasionally flooded with storm water. The growth of summer annuals with average rainfall and no flood water was short, and they matured little or no seed. Of the winter-growing species alfilaria and Indian wheat (*Plantago*) made good growth when the rains were favorable, and invariably matured seeds. Root-planting experiments were generally unsuccessful."

Wooton (1916:38) gives an account of reseeding studies on the Santa Rita Range Reserve which is in entire accord with that of Griffiths and Thornber:

"Practically all attempts to introduce new species of forage plants or to increase the relative abundance of particular endemic species beyond their natural importance in the plant associations of the region have resulted negatively. In a few cases introduced plants, like alfilaria or some aggressive annuals, have seemed to promise returns, but in the course of a few years the native perennials have crowded them out. The scattering of seeds of the local native species upon bare ground has proved to be well worth the trouble, since the practice has resulted in the more rapid recovery of such areas. This procedure has also put a crop of grass upon some soils where it was predicted that nothing would grow."

Introduction and reseeding have been generally successful in mountain meadows and other regions where the rainfall is relatively high, as well as in local areas of the sandhills and in river valleys where the water-content is above normal as a result of runoff or underground drainage. Griffith (1907: 22) concludes:

"Profitable partial cultivation of native pastures must be confined to productive areas in regions of sufficient rainfall to permit at least the occasional cultivation of some of the hardier crops. The areas where reseeding methods on an economic basis are applicable extend to the western plains, and are scattered throughout the mountains in meadows, high valleys, and other situations where the requisite moisture occurs."

Cotton (1908:23) states that experiments carried on in the mountain meadows of the Pacific coast "show that the carrying capacity can be greatly increased by reseeding with tame grasses. The grasses best suited to this purpose are timothy and redtop."

Vinall (1911:9), in discussing forage crops for the sandhill region of Nebraska, strongly urges that "a good percentage of clover be mixed with the native hay, as all the clovers grow naturally on the moist lands of the hay flats. In fact, no part of the United States seems able to produce clover with less care or attention than this wet-valley region, and its use here is strongly urged. Red clover seeded in 1895 in meadow sod, without plowing or other

cultivation, has reseeded itself from year to year in haying land, and is today in better condition and shows a better stand than ever before."

Prerequisites for seeding and planting.—The above accounts make it clear that water is the chief limiting factor in the establishment of seedlings or mature plants and that competition for water determines their persistence. Where the water-content is more or less in excess of the needs of the native population, as in mountain meadows with high rainfall, or in wet valleys with little drainage, tame grasses or forage plants can be introduced into the community successfully and without disturbing it unduly. Such areas constitute a relatively small amount of the total range, and they are rarely in such need of revegetation as the grasslands of low water-content. In dealing with the latter, the first great need is to take advantage of times of greater rainfall. This has generally been done with reference to the season, but no method has heretofore been available for anticipating periods of several years with rainfall above the normal. Such a method now exists in the use of the sun-spot cycle to determine the probable duration of the wet and dry phases of the 10 to 12-year climatic cycle. While the annual rainfall varies more or less during the wet phase, it is regularly higher than during the dry one. Moreover, drought periods of 2 to 3 years' duration have been found to fall only at the dry phase for the past 60 years. Hence, it is obvious that the difficulties attendant upon reseeding or introduction will be least during the wet phase and greatest during the dry one, and that all operations of this kind should be confined to the former. Moreover, it is especially desirable that sowing or transplanting be repeated for the first two years of the wet period in order that an adequate stand be secured in the event of the seasonal distribution of the rain being unsatisfactory. This would also accord with the probability of two or three fairly wet years for the proper establishment of the plants, before the beginning of the dry period.

A second prerequisite of great importance is the eradication of rodents. Where seeding is the method used, it is probable that the failure to secure a good stand is often due as much to the destruction of the seeds as to the lack of water. This is probably true even in the arid Southwest, since it is here that rodent damage is greatest. As a consequence, it is imperative to kill out the rodent population before seeding operations are begun on an area. It is almost as important to make sure that the rodents are kept out of such areas, since they may turn the scale against the establishment of plants which have germinated successfully. The food habits of the kangaroo-rat help to explain why the grama grasses fail to make seed and gradually disappear in the experiments mentioned above. In certain regions, at least, they would likewise render the establishment of transplants much more difficult. It is also obvious that areas in which reseeding is being carried on must be protected against grazing for several years. As a consequence, reseeding and transplanting should be fitted into the rotation system, and carried on with reference to the period of complete or partial rest given the different areas. It is assumed that all such operations must still be regarded as actual investigations and that they will be begun only where fencing assures control, and a preliminary study of conditions presupposes some degree of success. Under such conditions, it is possible to take the factor of competition into account also. The success attained in artificially reseeding bare and especially trampled

areas in pastures has been largely due to the absence of competition for water. When reseeding is employed to increase the density of an existing community or to introduce new dominants, competition becomes a critical factor. It can be adequately modified only in small pastures where disking or harrowing is economically desirable, or irrigation possible. On the ranges of the Southwest, with two growing seasons, it can be avoided by the use of winter annuals, which do not come into direct competition with the summer grasses at all.

New investigations.—In connection with grazing studies throughout the grassland and scrub climaxes of the West, it is proposed to extend experiments in reseeding and transplanting to all the associations. These are being established with especial reference to the prerequisites discussed and they have been planned for the next four or five years in the expectation that these will constitute the wet phase of the cycle. Protection and eradication have been emphasized, and particular attention has been devoted to methods of evaluating the rôle of competition, since actual practice will require the reseeding of both bare areas and overgrazed communities. This is done in protected inclosures, where tillage methods may be employed in so far as desirable, and where permanent quadrats can be maintaind for charting changes in composition and measuring the annual variations in yield (Clements, 1917, 1918, 1919). By the use of transplanting in addition to reseeding, it is expected to determine the ecological requirements of practically all the dominants and many of the subdominants, within the same association or local grouping, as well as between associations. (Clements and Weaver, 1924.)

In addition to improving the carrying capacity of overgrazed areas, it is hoped that it will prove possible to extend and develop mixed grazing types, such as the mixed prairie, and the mesquite and sagebrush savannahs. The mixed prairie has the highest carrying capacity of all grass types, and also possesses essentially the same high resistance as the short-grass plains to trampling, overgrazing, and drought. It owes this property especially to the presence of buffalo grass, *Bulbilis dactyloides*. The runners of this grass make it one of the very best for transplanting experiments and it should prove possible to establish sods as centers of ecesis throughout the grassland where the rainfall ranges between 15 and 30 inches. *Hilaria cenchroides* has similar values, but its range is more restricted and trials with it should perhaps be confined to the Southwest. The production of mixed prairies, and of all mixed types indeed, contains promise only in those climates or edaphic regions where there is some water-content in excess of the needs of the existing dominants. For this reason, it is practically certain that success can be attained only by transplanting short-grasses into tall-grass areas, or into existing mixed areas, rather than the reverse.

The value of mixed grass and palatable scrub in permitting the grazing of cattle and sheep, often with goats, and in providing a double insurance against drought or other disaster is so great that the possible extension or production of such types is of the greatest importance. In many cases it is expected that the carrying capacity of the type will be increased by replacing one shrub with another more palatable. Where savannah already exists or desirable scrub is already in contact with grassland, the extension of the scrub can be secured by a system in which grazing and fire are used to maintain the balance

at the point desired. Fire in conjunction with planting furnishes a ready means of developing grassland in the midst of scurb. The actual planting of shrubs in grassland is more difficult because the demand for water then tends to exceed the climatic supply. As a matter of fact, the demands of shrubs and tall-grasses are so nearly alike that shrubs can be readily introduced into true, subclimax, and mixed prairies during wet periods, as nature has often proved. Once established, their deeper root-systems and taller stems enable them to persist. Certain subclimax shrubs, such as the saltbushes, will probably permit similar treatment in moister situations in the short-grass and desert plains. Finally, the latter may be regarded as constituting a curiously mixed type in which the two elements, winter annuals and perennial grasses, occupy the same ground but become dominant at two different seasons. Since grasses depend almost wholly upon the summer rainfall for their growth, such a mixture is especially valuable in utilizing the annual rainfall to give the maximum amount of forage. While Thornber (1910) and others have emphasized the unique value of the winter annuals in the Southwest, their importance and the possibility of extending or developing this mixed type have not been generally understood. The chief annuals possess the vigor and the seed-production of weeds. Hence, the seeds germinate readily and the new plants quickly become established. Like all plants, however, they can not grow without rain, and their yield follows the variation in winter rainfall even more closely than grasses do that of the summer.

Forage development.—It is obvious that the utilization of hay and other forage to supplement the range during winter or periods of drought reduces the demand upon the range and hence helps to improve it. Fundamental as this is, it is far from a general practice among stockmen. While there has been utilization of native hay areas, few attempts have been made to develop them. Moreover, the use of native forage plants of an emergency character has been exceptional until recently, while the production of cultivated forage and silage crops by the stockman has barely been begun. Smith (1899:22) was the first to emphasize the importance of the production of hay and stack silage as aids to the improvement of the range. Thornber (1910:305) has discussed the use of methods for developing artificial meadows and fields by means of storm-water dams, but concludes that these are in general not very satisfactory. However, the majority of ranches perhaps contain areas on which a fair amount of native hay can be developed, or on which cultivated forage can be grown by means of irrigation, use of storm-water, or by the methods of dry-farming. This is especially true during the heavier rainfall of the wet phase of the climatic cycle. When the value of hay and silage as insurance against drought is fully realized, it will usually be possible to produce enough during the wet years to tide stock over drought periods. This is especially true of silage, because of the long period for which it can be kept. In view of the enormous difference in the production of forage crops in wet and dry years, it is imperative for the ranchman to realize that his most certain insurance against the disasters of drought is an adequate forage reserve. While increased hay production plays a part in this, maximum production of silage during the wet phase especially is much more important. Silage can be kept almost indefinitely in properly constructed silos, but it would probably never need to be kept more than four years, since even the most serious

drought periods have been only three years long. With the use of the method of climatic cycles to determine the approximate date and length of wet and dry phases, it will be possible to develop this drought insurance into a practical certainty. In the case of single years, it is a much more difficult matter to anticipate the probable rainfall, and during the dry phase additional insurance can be obtained by planting such forage crops as sunflower and Russian thistle. In fact, in the Southwest at least, it will be the part of wisdom to plant a certain amount of these every year, against the chance that the distribution of the rainfall may be abnormal.

Thornber (1911) and Griffiths (1905, 1908, 1909) have discussed in detail the utilization of native cacti as emergency forage plants and have shown how they can be cultivated in dry regions. The value of cacti as a supply of reserve food for drought periods is generally understood, but too little trouble is taken to see that it is available when needed. Other plants that are grazed little during wet periods but are eaten more or less by the cattle directly during drought are bear-grass or sacahuiste (*Nolina*), sotol (*Dasylirium*) and soap-weed (*Yucca*). The first direct utilization of any of these species as emergency forage was made by Mr. C. P. Turney on the Jornada Reserve in 1915 (Jardine and Hurtt, 1917:26). The critical nature of the drought period of 1916-18 gave an impetus to the development of machinery for chopping the plants into feed and resulted in a great extension of their use (Thornber, 1918; Wooton, 1918; Forsling, 1919). While they should be regarded strictly as emergency forage and not be permitted to take the place of proper forage development, there can be no question of their value as roughage in times of severe drought. If used as such, the supply in many regions of the Southwest is practically inexhaustible, but the tendency will almost certainly be to continue using soapweed in particular until it completely disappears from the accessible areas.

Water development.—The importance of water development for range improvement has been generally recognized and has been discussed in considerable detail by Smith (1899), Bentley (1898), Griffiths (1904), and Jardine and Hurtt (1917). These are all in complete agreement, and the conclusions of Smith and of Jardine and Hurtt are quoted in some detail, as representing the earliest and latest experiments in range improvement:

"Another precaution that must be taken, if the stock ranges are to be restored to anything like their former value, is that water must be provided in sufficient amount so that cattle will not have to travel long distances for it in times of severe drought. Nearly the entire western portion of Texas is underlaid by artesian waters ranging from 150 to 1,500 feet below the surface. Wherever the drainage slopes are not too precipitous, artificial tanks may be formed across the draws by building dams, and if the bottom of the tank is carried down to hardpan, or is puddled before being filled, a supply sufficient to last through the dry season may be secured at small expense. Such tanks, or wells, either artesian or where the water is lifted by windmill pumps, should be provided at least every 4 miles over the range, so that cattle will never have to travel more than a couple of miles to water. Where the wells, water-holes, or tanks are 8, 10, or more miles apart, as they very frequently are on some of the western ranges, cattle greatly overstock the range in the vicinity of the water, especially during midsummer, while the back country is thickly covered with good feed. Thus a portion of the range will be over-

stocked while another portion will be undergrazed. In the one case the grasses are eaten down and trampled for a few miles back from the water so that it may require several good seasons to undo the injury done in one bad year. In addition, the forage on the large area back from the water is entirely lost through not being grazed. The cost of constructing dams or providing windmills will often be but a small percentage of the loss incurred when no water is provided. It has been often observed that the period of flow of the rivers in countries which have been overgrazed is very much less than it was formerly. This is because the trampling of the herds has compacted the soil, and also because the waters are not retarded from running off the surface as they would be when the land is covered with a thick coating of grasses. Hence the drainage of the surplus water takes place in a very much shorter time. There are many streams and springs which in former years afforded a continuous supply throughout the dry season, which now only run during or immediately succeeding periods of abundant rainfall. Thus less dependence is to be placed upon the streams as a source of stock water. New artificial sources of supply must be provided." (Smith, 1899:26).

"Fairly efficient use of plains and mesa range in the Southwest can be secured where stock do not have to travel more than 2½ miles to water. This means one watering place for each 13,200 acres. Such an acreage of grama-grass range will carry about 500 cattle throughout the year if properly managed. As the distance in excess of 2½ miles which stock have to travel to water increases, the barren area around water increases, as does also the partly used forage beyond 2½ miles from water. Consequently the number of stock the range will support is reduced. When feed is short, a long distance between feed and water tends to increase the loss of stock, to decrease the calf crop, and to retard development of the young animals. Observations to date appear to justify one permanent watering place for each 500 head of cattle. Where conditions are favorable, the construction of tanks to catch flood waters for the purpose of supplementing the permanent watering places will be a paying investment. They will aid (1) in getting more green feed for the stock during the year, (2) in more even utilization of the range as a whole, (3) in the protection of feed and range near permanent water, and (4) in reducing the cost of maintenance and operation of wells." (Jardine and Hurtt, 1917:29.)

Herd management.—Better methods of handling stock may improve the range or prevent its deterioration directly, as in the open herding of sheep, or may be of indirect benefit, as in the production of a more efficient animal. Since the ultimate objective of range improvement is the maximum permanent production of stock, all methods which lead to this end are more or less concerned in it. While many of the factors in proper herd management have been worked out by the experiment stations in feeding and breeding experiments, the chief contributions to the management of range stock have been made by the Forest Service. These deal mainly with the handling of cattle in large range pastures, and of sheep in coyote-proof pastures and under new systems of herding. The immediate objectives have been (1) maintenance and improvement of the carrying capacity, (2) improvement in grade of stock, (3) increased calf or lamb crop, and (4) prevention of loss. The results secured on the Jornada Range Reserve have been summarized by Jardine and Hurtt (1917:30), as follows:

"The big opportunity for increasing the calf crop is to keep poor cows in thrifty condition. This can be done by not overstocking the range used by

breeding stock and by feeding a small quantity of cottonseed cake or other supplemental feed to the cows that need it. All bulls should be fed during the winter and early spring.

"The small loss at the Jornada reserve is attributed to careful, systematic vaccination against blackleg, to the reservation of grama-grass range for poor stock during the critical spring months, to feeding the animals a small quantity of cottonseed cake, and to prevention of straying.

"In order to provide for extra range for the breeding stock in poor years, one-third of the stock on a range unit should be steers. It is then possible to reduce the number of stock when necessary by selling steers, without great sacrifice and without interfering with the breeding stock. In good years the number of steers can be increased and in bad years decreased.

"To provide against loss in extremely bad years, some kind of roughage to supplement the range forage, for feeding with cottonseed cake or other concentrated feed, would be a decided advantage on southwestern ranges. Feeding cottonseed cake to calves weaned during the late fall, winter, and early spring is an important factor in cutting down loss and increasing the size of the stock, as well as in increasing the calf crop. Where this is done, young calves can be taken from poor cows, thus reducing loss from starvation among both cows and calves and stimulating earlier breeding."

The value of coyote-proof fences for sheep pastures and range lambing-grounds has been studied by Jardine (1908, 1911). His conclusions are that the carrying capacity under this system is about 100 per cent higher than under the ordinary one, and that the percentage of lambs is higher, the sheep are much better, the loss almost nothing, and the expense of handling materially decreased. The advantages of the "bedding-out," "blanket" or "burro" system of herding sheep have been studied by Jardine, Fleming, and Douglas, and have been summarized by Jardine and Anderson (1919:50). The latter have given the most complete account available of the management of cattle and of sheep on the ranges of the national forests, with respect to the range as wtll as the herd (pp. 30, 49).

ESSENTIALS OF A GRAZING POLICY.

A proper land system.—It has long been recognized by students of grazing that overgrazing and its attendant evils were the result of an unfortunate land policy. This fact has never been understood by the public, even in the West, and it is but recently that the stockmen themselves have realized it. A large portion of the country still holds the vague opinion that the West contains the possibility of unlimited homesteads, a delusion which western politicians and real-estate dealers have found it profitable to encourage. It is a national misfortune that the entire open range was not brought under adequate control at the time when the conservation movement was at its height, as the West contained few resources of greater importance. At present, every competent and disinterested student of the situation realizes that an adequate and just leasing system furnishes the only economic solution of the problem. The administration of the grazing lands upon the national forests has convinced the vast majority of stockmen of the advantages of leasing or allotment, and has dissipated the fears that the "little man" would suffer under such a system. In spite of this, public opinion has hardly advanced beyond that of the days of the "cattle kings," who were more or less

justly regarded as the foes of the homesteader. This is not to be regarded as strange in view of the failure of the West to comprehend the grazing industry as perhaps its major problem. When the West realizes, and causes both public and lawmakers to realize that half a billion acres of its land can never be used profitably for anything but grazing, it will become possible to enact the necessary legislation for an intelligent economic and social treatment of the public domain, such as was provided in the Kent grazing bill of 1913.

Essentials.—Coville (1898) and Smith (1899 : 43) have pointed out the essentials of a proper land system with respect to the needs of grazing, and Smith has summarized these as follows:

"The only way in which the non-mineral lands can be filed upon is either under the right of preemption, under timber claim laws, desert-land laws, or those relating to irrigated lands. There is no system for disposing of areas unsuited for agriculture other than under some one of these laws, and the result is that the grazing lands are held as commons open to any stockman who can run his cattle upon them. The first and foremost necessity, if the extravagant waste of the public domain is to be prevented, is to devise some system by which grazing lands can be placed in a class separate from agricultural lands, and under which property rights in lands now free to everyone may be assumed by individual stockmen. It has been the experience in all pastoral countries that proper care and conservation of the forage resources can only be secured and will only be practiced where the tenure of the land is sure. The necessary fixity of tenure might be legally provided for by long-term leases directly from the General Government at a nominal rental per acre.

"Aside from the effect of overgrazing on the lands themselves and on the natural grasses with which they are covered, it is well to note that millions of cattle and sheep are grazed on free lands in every Western State and Territory. These lands contribute no taxes for the support of the State governments. The cattle when marketed may be sold at a much lower figure than those raised on taxed lands owned by the stock grower and still make a profit. It is not fair to the people who are compelled to bear the expenses of local government for large untaxed areas, nor on the other hand to the cattle men and woolgrowers of the East whose products come into competition with those grown almost without expense on free Government lands. The policy which governed the settlement of the prairie States might well be modified to meet the demands of the stock raisers, especially as a very large percentage of the Government land now remaining is not agricultural and can not be made so by irrigation. The best policy is that which will the best promote permanent settlement. It is necessary that timely action shall be taken to open up the public lands for settlement in tracts extensive enough to encourage men to build ranches and make permanent improvements upon them. The continued existence of great bodies of free lands covered with free grass is demoralizing to all those who take advantage of the opportunities presented thereby. As suggested above, probably the most feasible plan would be to provide for long-term leases of the public lands for grazing purposes."

Classification and range surveys.—The necessity of a classification survey to determine the primary division of the public domain into agricultural, grazing, and forest lands has been discussed in the preceding chapter. Here it will suffice to emphasize the importance of classifying as grazing land all areas in which there is not convincing evidence of permanently successful

agricultural production. In view of the fact that dry-farming in many regions is largely confined to forage production, by far the best plan would be to treat the remainder of the public domain as grazing land and to organize it into districts and units in such a way that the forage areas could be intensively utilized.

The primary task of a range survey is to determine the grazing types and subtypes of a region and to approximate the carrying capacity of each. It must ascertain the character, composition, extent, and value of each type, as well as its present condition and its future development. It is essentially ecological in nature, and hence must be based upon the climax formations and their subdivisions, and upon their successional development. The most important unit is the grouping or faciation, which represents the local type with which an individual range must deal, though the larger ranches might have a number of different types. A range survey will necessarily devote much time to the need and the possibility of range improvement in the different types. It will pay especial attention to the indicators of overgrazing, and to the successional evidences of the best method of regeneration. It will locate the areas infested with rodents or with poisonous plants, and will suggest the most promising methods of eradication. It should likewise take note of all areas in which there is actual or potential development of hay and forage, and of the location and extent of communities of emergency forage plants. It must also deal with the possibilities of water development, by means of mills as well as by tanks. Finally, it will take account of sand-hill, bad land, and other areas in which some form of grazing reclamation is possible. In its complete expression the range survey should lead to the production of ecologic sheets and folios which would do for the range what topographic sheets and geologic folios do for the topography and geology of a quadrangle.

Production cycles.—The recurrence of wet and dry periods in general harmony with the sun-spot cycle has already been shown to have a profound effect upon the carrying capacity and water supply of the range. As a consequence, the climatic cycle is clearly reflected by a corresponding grazing cycle. The carrying capacity and water supply are high during wet periods, and they are at a minimum during drought periods. For successful ranch practice in the drier regions especially, the grazing cycle must be made the basis of a production cycle. In fact, it is already the basis of such a cycle, owing to the fact that production is necessarily reduced to the minimum during a drought period. It is imperative that the actual existence of such a cycle be recognized, and that its operation be anticipated and modified in such a way as to stabilize production. In existing practice, a series of wet years is a period of voluntary expansion, and a drought period one of involuntary contraction. With the increasing probability of forecasting wet and dry phases, the ranchman should make his plans accordingly. Expansion must still be the rule for wet phases, and contraction for dry ones, but the change from one to the other must be definitely anticipated and prepared for. This is particularly true of the critical change from expansion to contraction, but it is also true in a large measure for the reverse process.

Most of the essentials of a contraction-expansion system have already been discussed under range improvement. It is imperative to have the largest

possible amount of insurance against drought in the form of rotation grazing and reserve pastures, and of water development. Even greater possibilities of adjustment are afforded by the management of the herd to secure necessary contraction and desirable expansion. On the Jornada Reserve this has been obtained by maintaining the number of steers at about one-third the total of the herd, but increasing the number in good years and decreasing it in bad years as the range warrants or demands (Jardine and Hurtt, 1917:31). Still greater elasticity is provided where it is possible to employ mixed grazing, running cattle and sheep together, or cattle, sheep, and goats. Mixed grazing not only permits readier adjustment to climatic conditions, but also serves in some measure as insurance against unfavorable market conditions.

Ranch management surveys.—The task of placing the grazing industry upon a sound economic and social basis is not solved until costs of production can be determined. Until this is done and net income ascertained, it is impossible to know the efficiency of any particular ranch in either economic or social terms. It is felt that the only proper objective of any production system is to secure an equitable balance between the needs of the producer and the consumer. Such a balance is possible only when the actual cost of production is known, so that its relation to the proper cost can be determined. In its present condition the stock industry of the West is little better than a game of chance, in which both the stockman and the public are regularly losers. It can be converted into a productive business that does its full duty to the individual and the nation only by means of proper land legislation, adequate methods of range improvement, and by ranch management surveys, which will disclose the exact status of each ranch as a productive unit. Such surveys may well serve to usher in a period of cooperation in ranching, which will make possible great improvements in range and herd management as well as in marketing and distribution. They would probably lead also to the stabilization of land values and the reduction of interest rates, and to the production of social values such as rarely obtain at present.

XVI. FOREST INDICATORS.

Nature.—Forest indicators are of three chief types, namely, (1) those that have to do with existing forests; (2) those that indicate former forests; (3) those that indicate the possibility of establishing new forests. A community of trees is axiomatically an indicator of forest, but it carries with it indications of habitat, structure, and development which are not so obvious. Moreover, it involves important indications as to use, such as lumbering, water regulation, grazing, etc. Indicators of former forests are either actual relicts of the forest itself or seral communities which mark particular stages of the successional reforestation. They may consist of the dominant trees as individuals or communities, of the subdominant shrubs or herbs of the climax forest, or of the dominants or subdominants of any successional stage. Their great value lies in the fact that they not only indicate the possibility of reforestation, but also the stage which has been reached and the further methods to be employed. They are by far the most important and practical of all forest indicators when the vast extent and significance of deforested areas are taken into account. They pass more or less gradually into indicators of the possibility of forest production in regions which have been repeatedly deforested and which show neither relicts nor seral stages of the original climax. Such are the transition regions between forest and scrub or prairie, in which the latter appear to be climax, but are really subclimax and will consequently yield to forest when artificial regeneration is employed. In addition, chaparral and grassland may also indicate afforestation in regions which have not borne forest for hundreds or thousands of years. These are primarily edaphic areas in which the indicator community owes its presence to a higher water-content resulting from soil or topography. Such are the sandhills of Nebraska and the river valleys throughout the prairie associations.

Kinds of indicators.—Both the individual and the community may be used as indicators. The latter is naturally more complete and definite, but in many cases the change following clearing or fire is so complete that a single relict individual gives information of great value as to the original climax. This is true also of subclimax forests which have more or less completely disappeared in the reestablishment of the climax forest. The forest formation which is climax for a certain region is itself the indicator of the permanent type of the region, and hence of the forest which will naturally develop or redevelop in all bare or cleared areas. As a consequence, it is an indicator of site and likewise of the type of management to be employed. Each association is an indicator of climate, while the various groupings and alternations of the consociations indicate different edaphic conditions as well. The societies indicate variations in water-content or light primarily, but the layer societies are especially related to light. Differences in the density and growth of dominants and subdominants serve as indications of minor changes in the factor complex. Indicator values may be derived from growth in height, diameter, or volume. The former is the most convenient for use, but the latter is probably the most accurate. Seedlings are among the best of dominant indicators, especially when their growth, habit, and abundance are taken

into account. The minute structure of leaves is an excellent indicator of light and water relations, and that of stems is an indicator of annual fluctuations in rainfall, and hence climatic cycles. Flowering and seed-production also have their indicator values, but these are of secondary importance.

Seral communities differ chiefly from climax ones in indicating edaphic conditions or habitats rather than climate. Their peculiar value lies in the fact that they may at the same time indicate the nature of the initial area or disturbance, the particular stage of development in the succession and the habitat, and the final association or climax. Such stages are denoted by the associes, and minor stages or variations by the consocies, while the socies denotes subordinate differences within these. These three types of community, and the series of associes which constitute the sere, form a complete scale of variations and changes, upon which the problems of forest maintenance, of reforestation and afforestation, must be based. In short, while the climax indicates the permanent forest of a region, the seres indicate the methods and materials which must be used in hastening, maintaining, or postponing the climax community, which is inevitable under natural conditions. It is obvious that seral communities furnish indications from composition, density, and growth essentially similar to those of the climax.

FOREST TYPES.

Bases.—The nature of forest types and the bases for their distinction have been fruitful subjects of discussion among foresters. Graves (1899) seems to have been the first to characterize forest types definitely:

"If nature is left undisturbed, the same type of forest will tend to be produced on the same classes of situation and soil in a specified region. There will be variations within the type, but the characteristic features of the forest will remain constant, that is, the predominant species, density, habit of trees, reproduction, character of undergrowth, etc. If a portion of the forest is destroyed by fire, wind or otherwise, the type may for the time being be changed, but if left undisturbed, it will revert to the original form, provided the condition of the soil is not permanently changed."

Zon (1906) states:

"The first step in any silvical study or attempt at forest management is to reduce the great variety of stands to a small number of types, each having characteristic features of its own and requiring a distinct treatment. The nearer we come to establishing natural types of forest growth, the deeper we penetrate into the true relationship existing between these types and the factors that produce them, and this is the most important contribution to silvics."

The changes brought about in a forest by man or by accidents are not regarded as a basis for the establishment of fundamental forest types, but it is recognized that such changes do produce temporary or transient types. The essential agreement of the basis proposed by Graves and Zon with the principles of succession and the distinction between climax and developmental communities was pointed out by Clements (1909:62):

"Reproduction is the forester's term for development or redevelopment; it is the complex response of a formation to its habitat, which leads to succession. The result of reproduction is a forest type of succession, an ultimate or

stable formation, i. e., a forest type and a stable formation of a succession are identical. This identity is made clearer by the author's insistence upon stability as the ideal for which the forester must strive in regenerating and caring for his forest. The change in stabilization is perhaps the most essential feature of a succession, and the succession terminates only because the habitat is finally occupied by a formation which, accidents excepted, is best suited to it and hence is permanent."

The varying concepts and applications dealing with the forest type are well illustrated by a symposium on the subject, the papers of which are briefly abstracted here. Dana (1913: 55) defines the different kinds of types which seem to serve a useful purpose and should be recognized:

"A *forest type*, known often as simply a *type*, is a stand of trees with distinctive characteristics of composition. A *cover type* is a forest type now occupying the ground. The term conveys no implication as to whether the type is temporary or permanent, or one which we shall strive to maintain under forest management. A *temporary type* is a forest type which has come in as a result of some interference with natural conditions, such as fire or lumbering, and which will eventually, if nature is left undisturbed, be replaced by a different type. A *permanent type*, or *natural type*, is a forest type which will eventually take possession of and perpetuate itself on any given area if natural conditions are undisturbed. A *management type* is a forest type that we shall strive to maintain under forest management, irrespective of whether or not it is the type that would occupy the area under natural conditions."

Munger (1913:62) emphasizes the following points:

"The term forest type must above all be used for a classification of timberland that will be useful to the practicing forester in forest management in a broad sense. Forest typing must not merely be a theoretic grouping of similar areas convenient for wall-map purposes or a classification of merely botanical or ecological interest. Their distinctions must be based on fundamental points of difference which have significance to the forester. In every form of intensive reconnaissance which a forester is doing preparatory to making working plans, he should include the collection of data showing both the present composition by species and the physical conditions of the site. Though both of these classes of data may be shown on his maps, I feel that the term 'forest type' should be reserved for a classification based upon permanent basic physical factors. I should define, therefore, a forest type as an aggregation of areas of forest land upon which the physical conditions of climate, soil, and moisture are so similar that an identical form of silvicultural management may be applied on all."

Woodward (1913: 69) states:

"In the examination of lands offered for purchase under the Weeks law, it has been found desirable to classify the kinds of forest stands and sites from two points of view. In the first place, it is necessary to know the composition of the present stands in order to arrive at the value of the timber. The second way in which sites need to be classified in valuing the lands offered is to determine the value of the site for producing timber. In a virgin stand, the present composition is a very good index of what can be grown on the area in question. However, it is conceivable that under forest management it may not be advisable to wait for the struggle for existence to proceed so far that temporary species are eliminated. As a means of classifying stands and

sites, a system of types and subtypes is now in use. A forest type is understood to be an area in which the climatic and soil factors are uniform and which may therefore produce stands of like composition. A subtype is a subdivision of a type in which the struggle for existence is not yet completed and whose composition is therefore changing. Generally this temporary condition is caused by fire, lumbering, windfall, etc. The most common species in subtypes are light-needing ones which occupy the ground quickly, but which will ultimately give place to more tolerant species."

Moore (1913: 75) summarizes his views of forest types as follows:

"A forest type is a tree society having such differences of composition from other tree societies as to make necessary a separate study of yield. Physical factors are the cause of forest types, but not forest types themselves. They cause confusion when used in classifying forest types. Yield studies are at the foundation of forest management, and must be based on forest types distinguished by composition. Reconnaissance must furnish material to which yield studies can be applied. For this purpose it must distinguish forest types by composition, whatever other method may be used in addition. Fortunately, this is, for most regions, the easiest way of distinguishing forest types."

Greeley (1913: 76) points out:

"There have been three general stages in the work of the Forest Service, each involving a somewhat different point of view in the classification of forest types. During the first stage the 'cover type' in its simplest terms was adequate. In the second stage, the 'cover type' in itself is inadequate. We need rather the 'management type.' In the third phase of the work to which I have alluded, we need possibly an additional type—the 'physical type' or 'land type.' The type needed for the classification and description of National Forest lands is the 'management type.' The classification of forested areas should be attacked from the standpoint of what those areas will grow best under scientific administration. Let us have, then, a classification of forest types based upon present cover interpreted where necessary by the uses which we will make of it in management. Let us leave the intensive study of physical factors to the working-plan expert or the silvicist. The 'management type,' in my judgment, is the key to the classification of complex stands arising from changes in composition at different periods in the life-history of the forest. I would apply this principle to any complex situation where a temporary type is followed by a permanent type, selecting for the purposes of our classification the stage in the natural rotation of species which, as far as we can now see, will be the basis of the forest management. In a word, the existing cover interpreted by our knowledge of the life-history of the type and of what the land should produce under management will, I believe, furnish the best basis for classification."

Pearson (1913: 84) emphasizes the value of communities as indicators and summarizes the bases for the classification of forest land into types, as follows:

"The only scientific basis for such a classification is that of potential productiveness, considering both agricultural and forest crops. The productive value may be ascertained in two ways: The first measures directly, as far as possible, all physical factors on the site and gauges the productive capacity by the measure in which the sum of these factors meets the requirements of various crops. The second method uses characteristic forms of vegetation

on the ground as an indicator of the physical conditions present, and upon this basis ascertains the adaptability of the site for different crops. The obvious objection to the first method is the need of climatological data and soil analyses on each site to be classified; and, owing to the diversity of sites in our forest regions, together with the almost entire absence of climatological records in many sections, the collection of data would involve an expense which, at this stage of our advancement in forestry, would be almost prohibitive. The second method requires a thorough preliminary investigation in each region to be covered, in order to secure a working knowledge for the actual land classification, and obviously reliable results can only be obtained by the employment of trained men. This method is the simpler and probably the more reliable of the two, and it is considered entirely applicable to the needs of the forester."

Rockwell (1913: 85) defines four types, as follows:

"The *temporary type* is a transitional condition, in which a forest of a temporary character is established as a result of some disaster which overwhelmed the original stand, but which will, if the disaster is not repeated, in time revert to the original climax form. The *climax type* is named for the species which will eventually predominate as a result of the physical factors concerned, provided the stand is left indefinitely undisturbed. The *cover type* may be either temporary or permanent; in mature and over-mature stands the name is based on the present composition; in immature stands it is based upon the probable composition at maturity. A fundamental type which, similarly to the climax type, is based on physical factors of site, but named for the commonly occurring species most important from a management standpoint, instead of for the climax species, will here be called, for want of a better name, the *'physical type.'* In addition to furnishing a better basis for the estimate of future yield and the regulation of the annual cut, the knowledge of site conditions which a 'physical type' map supplies is of great assistance in handling all the problems of forest management. After the types have been thoroughly studied, we will know definitely the range of climatic conditions in each type—knowledge of great value in forestation, fire protection, and land classification work. We will know what species can grow in each type, their rate of growth, and what they will yield. We will know about the behavior of different species within the type, and can then plan intelligently the management of cutting operations, methods of brush disposal, and other problems of forest management. Not until the physical types are properly classified and mapped can these problems be definitely worked out."

Mason (1913: 91) recognizes—

"Two classes of forest types. One of these types is based upon physical factors and will be called the 'physical type'; the other, based on the forest cover found on the area in question, will be called the "cover type.' A physical-type map is principally valuable in forest management to indicate the species which can be grown most profitably on a given area. It is useful in case planting is to be done, or if a method of cutting merchantable timber is to be selected which will reproduce the proper species. A physical-type map, then, shows the potentialities of the area mapped. It need show nothing with relation to the present forest cover, or even the presence or absence of forest growth. The cover-type map, on the other hand, shows whether or not the area is timbered at all. It shows what kind of timber is now present on the area and its age. In indicates the nature of the crop which will be

harvested during the present rotation. The physical-type map, then, shows what the land is capable of producing, while the cover-type map shows what the land is producing. If the cover type is important in connection with the present rotation, the physical type is important with relation to the next rotation. The physical-type map indicates the species which may be best grown upon a particular area. This, however, is a matter of comparatively secondary importance in forest administration. Furthermore, questions as to proper species for planting and suitable methods of cutting are solved by special studies rather than in the course of the work of the general reconnaissance crew. Physical-type maps are doubtless of great silvical and ecological interest, but cover-type maps are more valuable at present to the men who are managing forests in a practical way."

Tillotson (1913:95) has emphasized the importance of permanent forest types:

"Ordinarily it is undoubtedly true that better success will attend silvicultural operations if due regard be given to the establishment and maintenance of permanent forest types. It therefore becomes important to learn to distinguish and to classify them. It seems that this will necessitate the division of the country into rather large areas, over which the same general conditions of temperature prevail at similar altitudes, these units to be subdivided into smaller areas, where similar conditions of precipitation both as to amount and distribution exist, and these still further into smaller units, where differences in exposure, topography, or soil exist. On similar areas of this last division the ultimate forest growth may be expected to be the same, both in composition and in character, and it makes little difference in speaking of the permanent types whether they are called, for instance, the north-slope and the south-slope type, or the north-slope Douglas-fir type and the south-slope Douglas-fir type, providing the character of the growth in the region under discussion is known. The physical factors of the habitat will determine the type, and if these are known the character of the ultimate growth will be known by one familiar with the region. To one not familiar with the region any designation of types will in any case necessitate a description of them."

Zon (1913:103) points out:

"One of the most urgent and fundamental silvical tasks of the present moment is the working out of a natural classification of our forests. Since there are no characteristics within the stands themselves which could be used as unmistakable guides for dividing the forest into homogeneous silvicultural units and for acquiring exact knowledge of their silvical requirements, one must necessarily seek such characteristics outside of the stands. Such guides are found in the external environment, with its climatic and soil peculiarities. These alone determine the composition and combination of the species as well as the silvical requirements of the stand. It does not make any difference whether the name of the forest type is derived from the distinctive commercial species or topography, provided that in differentiating the forest into types the physical conditions of growth, which are the fundamental and primary causes of the real differences in the stands, are taken as the basis. If forest types are based upon physical conditions of growth, they will necessarily also determine the character of growth and make superfluous the further subdivision into quality classes.

"In a proper forest classification, two things must be distinguished: (*a*) types of forest as the product of physical conditions of growth, and (*b*) the

condition of the stands as the product of the interference of man or natural accidents. In the latter group will belong temporary types—sprout forests, abnormally open forests, the absence of undergrowth on account of grazing, etc. The classification into types is fundamental and is of importance not only for the present but also for the remote future. Classification on the basis of secondary characteristics, which are merely stages in the evolution of the type, is important only for the immediate future.

"A comprehensive classification of forests into types should begin by establishing, first, silvicultural units of various orders. The country as a whole should be divided into botanical-geographical regions—as, for instance, northern conifers, central hardwoods, etc.; each region must be subdivided further into subregions—thus the northern conifers into spruce subregion, pine subregion, etc. Within each subregion the forest should be divided on the basis of marked differences in topography and geology into types of forest massives. Each forest massive should then be divided into forest types, and within the boundaries of each type the stands may be further grouped by age, by origin, or by any other distinction which may be due to the interference of man or accident.

"Without denying the importance of the secondary characteristics in describing and differentiating forest stands, these characteristics must be placed, it seems to me, in a different perspective—at the end and not at the beginning of the work. All attempts at forest classification so far made have been based either upon artificial characteristics or upon characters in which the interference of man was not separated from the natural factors. Such a classification inevitably included in one group stands extremely heterogeneous silviculturally. In order to secure a natural classification and at the same time a complete knowledge of the silvical requirements of the stand, it should embody in the classification both the natural characteristics and the characteristics produced by the interference of man, but subordinate the latter to the former—that is, the characteristics produced by man should be used for classification only within uniform conditions of growth—the physical conditions for growth for the same type must be so similar as to guarantee a biological uniformity of stands."

Comparison of views.—A careful scrutiny of the opinions just summarized makes it evident that they differ more in emphasis than in fact. While the majority prefer to make use of the community, either actual or potential, they do this as an index to conditions and management. Those who regard the physical factors as the most important recognize the necessity of knowing the composition. The fact that the physical type is defined as one in which the climatic and soil factors are uniform shows that even this view takes proper account of the community, since there is at present no other measure of the uniformity of the factors concerned. In fact, practically every author regards both habitat and community as essential to the adequate understanding of forest types, and this agreement extends also to the desirability of recognizing and using various kinds of types. This is especially true with respect to permanent and temporary types, and largely also for management types, all of which may be cover types, when the community is emphasized. They are likewise physical types when the chief emphasis is placed upon the habitat or site, but technically, temporary types would usually be excluded. It thus becomes clear that forest types must take full account of both habitat and community, and that the community is the visible sign of any type. It is the indicator of the physical factors of the site as well as of the kind of

management which such a community demands to produce the maximum return. In short, it is the indicator value of the community, which the forester, consciously or subconsciously, has constantly in mind when he is defining or classifying forest types. As a consequence, the major objectives of forester and ecologist are the same in the study of vegetation, and the system of classification and of indicators which the latter establishes as the result of successional and quantitative studies should be equally serviceable for the former.

Forest sites.—To the ecologist it seems that much confusion has resulted among foresters from the fact that they have constantly used the indicator method, but usually without a clear recognition of this or of its connotations. As a consequence, there is frequent doubt as to the meaning of the terms type and site. The causes for this confusion have been discussed by a number of foresters. Dana (1913: 58) points out:

"The use of the term 'physical type' in this sense is practically the same as the generally accepted meaning of 'locality' or 'site.' This is defined in Forest Service Bulletin 61 as 'An area, considered with reference to forest-producing power. The factors of the locality are the altitude, soil, slope, aspect, and other local conditions influencing forest growth. Locality class, or quality of locality, includes all localities with similar forest-producing power.' Such a classification is undoubtedly a useful one for many purposes, but it would be better to drop the misleading term 'type' and to substitute for it either of the approved terms 'locality' or 'site.' In any event, it should be clearly understood that the term refers to the area and not directly to the stand."

Moore (1913: 75) says:

"The main point at issue becomes, therefore, one of terminology: Shall we call the environment or physical factors a 'forest type,' or shall we apply the term 'forest type' only to the tree growth? It is evident that we require a separate term for each. Common usage in this country has generally made the term 'forest type' apply to the forest cover. It would therefore simplify matters, I believe, if some other term such as 'site' were recognized as applying to physical factors, while the term 'forest type' is reserved for the forest cover."

The argument for a clear-cut distinction between forest type and site receives strong support from a comparison of the statements of Moore and Zon. The former (*l. c.*, 75) states:

"Mr. Zon, in his article 'Quality Classes and Forest Types,' uses the term 'forest type' to indicate environment or the sum of all physical factors; used in this sense, the 'forest type' becomes synonymous with site quality."

Zon (1913: 102), however, merely says:

"An attempt to use such site classes for forest types as an expression of the physical conditions of growth must necessarily lead to confusion."

Zon's further conclusions as to forest types and site classes have a direct bearing on this question:

"The division of a forest into stands having different average heights or site classes is perfectly justifiable as long as the end sought is purely an economic one. Site classes based upon the average height of the stand can

not always represent physical conditions of growth, as the same site classes may be found in stands which have entirely different physical conditions of growth, in other words, belong to two distinct forest types. Site class, therefore, while it indicates the actual character of the timber found on the ground, is not a silvicultural unit which can be used in management. The average height of the stand or site class may be the result of the interference of man, fire, animals, etc., and for this reason can not always be taken as the true measure of the productive capacity of the soil, even within the same type. The classification of stands on the basis of their average height is still further deceptive, because it does not take into effect the taper or the soundness of the timber, two qualities closely connected with the physical conditions of growth of the stand. The use of quality classes alone as indicators of the physical conditions of growth is as misleading as to use the composition of the stand for determining forest types. Both at best show only the actual condition of the stand, but are entirely mute as to the physical factors that are the cause of it."

The question of sites and their recognition has received much attention at the hands of foresters. It is essentially a matter of indicator values, in which growth, or its consequences, furnishes the indications desired. For this reason it is discussed briefly in a later section on growth as an indicator.

Succession as a basis.—A complete and satisfactory solution of the forester's difficulties in the recognition and use of types and sites is possible only on the basis of successional studies. Succession at once removes the confusion between sites and types, since it emphasizes the basic relation of the two as cause and effect. The site or habitat is the controlling cause and hence the explanation of the type or community, but is itself reacted on by the latter in such a way that it passes through a number of developmental stages to the final climax condition, each stage marked by its characteristic community. An adequate study of the community can no more neglect the habitat as cause than it can the community as effect, and also as the cause of modifications in the habitat. Moreover, it leads to confusion in the minds of others to use such terms as physical type and cover type, which appear to ignore one or the other. This is abundantly shown by the opinions cited above, in which essential uniformity is often completely hidden by superficial disagreeement.

But succession does not merely put type and site in this proper relation to each other. It is even more important in furnishing the only basis for the natural classification of types, and hence of sites also. Other bases may be natural in some degree, depending upon the criteria used, but development is the only one which takes into account all the factors and processes concerned and in their proper relation (Plant Succession, 111). Its essential feature is the recognition of the forest as a complex organism with a characteristic structure and development. The mature or adult stage is the climax forest while its development is represented by a series of typical stages or communities arising in bare or denuded areas. The climax communities correspond with permanent types, and the developmental or seral ones with temporary types, while both are cover types where they actually occur on the ground. The management type, whatever its name may be, is peculiarly successional in nature, since it depends not only upon the climax and its succession, but also upon the degree to which the latter can be controlled in the interests of optimum production.

The greatest importance of the successional basis for the classification of forest types lies in its indicator values. The climax communities of different degree are the indicators of the climates and subclimates, while the seral communities indicate soil and other local or edaphic conditions. At the basis of succession lie competition and reaction, and within the control of the climate, these are the forces which largely determine the density and growth of stands. But even greater indicator values inhere in the sequence typical of succession. Each stage indicates not only its particular habitat, while its variations in composition or structure indicate similar variations in the controlling factors. In addition, it serves to indicate communities and habitats which have preceded it, and those which will follow it. Seen in its successional relation, each community or cover type is an indicator not only of physical conditions, but also of the past history and future possibilities of the area concerned, and hence of the system of management or of planting.

Significance.—The primary value of forest indicators lies in denoting the physical factors in control. The climax communities of different degree indicate the corresponding climates and their subdivisions. The seral communities indicate local or edaphic conditions, usually of water-content, and at the same time mark the presence of progressive changes due to reaction. The dominants of both climax and seral communities serve to measure the light relations, and this is especially true of tree seedlings and of the subdominants that form the societies of the forest floor. Processes, such as fire, lumbering, grazing, etc., that produce disturbance, are either marked by relicts of the original vegetation, or by subseres more or less typical of the particular process. Growth is one of the most sensitive and hence one of the most important of indicators in the detailed study of communities and stands. Furthermore, the climax and the seral stages of a region taken together determine the general type of management possible or desirable. The composition and successional position of the community in any particular spot furnish a clear indication of the type of management necessary to the utilization of a certain species or stage as the preferred crop. Since succession is essentially progressive in nature, the maintenance of a particular crop or rotation depends upon a knowledge of the competition and reaction of the dominants, and the relation of these to the successional movement. In any climax, there will be seres in all possible stages of development. Some of these will need to be held in the present stage, while in other cases the progressive movement must be favored or hastened, and in still others it will need to be retarded. Whatever the desired method, when the dominants in possession are used as indicators of the forces which initiate and maintain the succession, it becomes possible to adjust the system of management to all the differences in composition and development.

CLIMATIC AND EDAPHIC INDICATORS.

Climatic indicators.—It is axiomatic that all forest climaxes are indicators of forest climates. The four western formations, woodland, montane forest, Coast forest, and subalpine forest, indicate as many corresponding forest climates, while the scrub formations and especially the chaparral indicate climates in which water conservation is important. It is well understood that the three mountain climaxes indicate climates with a progressive, increase

of rainfall from woodland to subalpine forest, while the Coast forest has the highest rainfall of all. In similar fashion, woodland, montane, and subalpine forest indicate a progressive decrease in the length of season and the temperature values, though the Coast forest marks the longest growing season and the most equable temperatures. The rainfall and temperature relations of the several formations have already been suggested in "Plant Indicators" (105) and need not be repeated here. The associations indicate subdivisions or subclimates of the formational climates. In general, the Petran associations are drier and colder than the Sierran associations of the montane and subalpine climaxes. For the three woodland associations, the total rainfall varies less than its seasonal distribution, and the temperature relations seem more decisive than the rainfall. The piñon-cedar indicates the coldest climate with much of the precipitation as snow, the oak-cedar the warmest, and the pine-oak the most equable. The first two have from 40 to 70 per cent of their rainfall in the summer, and the latter about 20 per cent. The two associations of the Coast forest show two subclimates strikingly different in both rainfall and temperature.

The consociations serve to indicate still finer climatic divisions, both as to altitude and latitude, though in general their indications are merged in those of the association or formation to which they belong. This is well illustrated by the montane forest, in which *Pinus ponderosa* indicates drier and warmer climatic conditions than *Pseudotsuga mucronata,* while *Abies concolor* is more or less intermediate. Consociations also indicate potential climates, with especial reference to the wet phase of the climatic cycle, where they form savannah, as in the case of *Pinus ponderosa* in the grassland climax, or *Juniperus* in the sagebrush. The varied groupings of consociations throughout an association also have some climatic indications, but these are often obscured by edaphic indications of more importance.

Two outstanding investigations have been made of the physical factors of climatic types. The first is that of Bates, Notestein, and Keplinger (1914: 78), the second, that of Sampson (1918). The former deals with yellow pine, Douglas fir, and Engelmann spruce groupings of the central Rocky Mountains. The factors of the air and soil were measured during 1910-1911, and the following conclusions were reached as to the differences of the several types:

"There are wide differences in the heat requirements of the species and in the temperatures of the types. The types vary somewhat in air temperatures, but much more distinctly in soil temperatures. The length of the growing season as determined from soil temperatures is a fairly accurate basis for determining what tree should be grown on the site. It is possible that after a series of careful observations a rule may be laid down by which the growing season may be determined from a very few soil-temperature measurements, or a direct relationship between the degree of solar radiation at any time and the length of growing season may be established. This last, of course, will simply be a scientific method for 'sizing up' the combined effects of slopes, aspect, and altitude—a thing which is done roughly by the forester every day.

"The soil moisture of the types varies greatly, the spruce requiring the most and the pine the least soil moisture; but the soil-moisture percentage is not a good basis for comparing types except in the same immediate vicinity, where it is known that the physical properties of the soils are uniform. In

any locality the spruce type probably always receives a greater amount of precipitation than the pine, and if all sites had the same aspect and gradient the amount of precipitation might determine the type. There are, however, too many influences affecting the final value of precipitation to make this element a safe criterion.

"From the above it is readily seen that the measurement of soil temperature affords the simplest means for determining the qualities of the site. In this measurement are involved the effects of the slope and aspect; the direct or indirect solar insolation; the effect of retained snow or precipitation which cool the soil; the effect of wind movement and humidity as they may cause evaporation from the soil, and the effect of wind movement as it may bring heat or cold from areas of different temperature."

Sampson (1918: 69) has determined the physical factors of the chaparral, montane, and subalpine associations of the Wasatch Mountains in central Utah, employing standard plants as well as instruments for habitat analysis, and showing the differences with respect to the various factors and responses in graphic fashion. His general conclusions are as follows:

"The mean annual temperature increases gradually from the highest to the lowest type, and this results in the longest growing season in the lowest type and a gradual decrease in the period of growth with increase in elevation. Thus from the time of the beginning of growth to the occurrence of killing frosts there are about 120 days in the oak-brush type, 105 in the aspen-fir type, and 70 in the spruce-fir type.

"The normal annual precipitation is greatest in the aspen-fir association, but is only slightly heavier in this association than in the spruce-fir. Less than half as much precipitation is recorded in the sagebrush-rabbit-brush as in the aspen-fir association; and in the oak-brush type it is only slightly greater than in the sagebrush-rabbit-brush type. The precipitation is rather uniformly distributed throughout the year.

"Of the three associations critically studied, the evaporation during the main growing season is greatest in the oak-brush type; but owing to high wind velocity in the spruce-fir type the evaporation is nearly as great as in the oak-brush type. In the aspen-fir type the evaporation factor is notably less than in the types immediately above and below. This is accounted for largely by the lack of high wind velocity, which is due to the luxuriant vegetation and to topographic features.

"In the case of all species employed, the total, and, indeed, the average leaf length and total dry weight produced are notably greatest in the aspen-fir association, these activities being rather similar in the spruce-fir and oak-brush types. The decreased production in leaf length and the production of dry matter in the respective types are in direct proportion to the evaporation.

"The elongation of the stem is greatest in the oak-brush type, intermediate in the central type, and least in the aspen-fir type. Thus stem elongation appears to be determined largely by temperature and seems to be little influenced by the intensity of the evaporation.

"The efficiency of the leaves per unit area as manufacturing agents, that is, in the production of dry matter, appears to vary inversely with the evaporation, though, indeed, temperature appears to be one of the important factors. The largest amount of dry matter per unit of leaf area is produced in the aspen-fir type and the least in the oak-brush type, while in the spruce-fir type, where the evaporation is only slightly less intensive than in the oak-

brush type, the dry matter produced is only slightly greater than in the oak-brush type."

Edaphic indicators.—These are either climax or seral dominants and subdominants. Seral dominants are typical edaphic indicators, since they mark the changing conditions of the habitat in its progressive development to the final climax condition. Climax dominants differ in their requirements and necessarily show indicator responses to local edaphic as well as general climatic conditions. Subdominants, whether seral or climax, mark minor differences in the habitat, and serve also to indicate the dominants in many cases where these have been destroyed or removed. The most striking edaphic indicators are the seres which arise in bare or denuded areas. Each prisere not only marks a particular type of initially bare area, such as water, rock, or dune-sand, but it also indicates the changes of the habitat complex, as well as the final climax. As already mentioned, each seral stage or community indicates a certain set of factors, and at the same time the stages which are to come in the development of the climax. This is likewise true of subseres, which differ from priseres chiefly in arising in areas denuded by fire or other accident, or by the agency of man. They are much more numerous than priseres, the successional movement is much more rapid, and the stages fewer. Each subsere is an indicator of the disturbance process that originated it, and its stages mark the different degrees of development of community and habitat on the way to the climax. Such stages, or associes, occur in both subsere and prisere. Each marks a particular stage of the habitat which controls it, and in turn reacts upon the habitat to produce the next stage. It consists of two or more consocies, or seral dominants, which indicate minor changes in the stage and hence perhaps different areas of habitat. In addition, each seral community contains a varying number of subdominants which constitute socies, corresponding to the societies of climax communities. The socies mark the more minute differences of the habitat, and perhaps also the minor movements within the associes.

The most important edaphic indicators are those which denote differences in water-content, light, or soil, or mark the effect of disturbing agencies, such as fire, grazing, etc. In addition to the presence or composition of a community, its growth or the growth of one of its dominants serves as an indicator of variations in the habitat complex or of site quality.

Water-content indicators.—In the several forest climaxes, the physical properties of the soil in relation to water-content are so much more important than the chemical that the latter require little attention. As a consequence, the indicators of water-content serve as indicators of soil texture, aeration, and temperature as well. The water relations of the climax and subclimax dominants have been considered briefly under each forest association. The climatic relations of the dominants of a community are reflected in the edaphic ones, and this may even be true of the dominants of different formations. The dominants of drier climates or subclimates take the drier slopes and ridges of the local area, and those of moister climates grow on northerly slopes and in canyons or valleys. *Picea engelmanni* frequently reaches the lower limit of the montane forest along the moist canyons of north slopes, while *Pinus ponderosa* extends to the middle of the subalpine forest zone or

even higher on dry and warm south slopes. In short, dominants indicate the total water relation, and hence their climatic indications may be completely subordinated to local conditions.

It is assumed that all dominants have different water requirements, and that each in consequence indicates a different water-content. It is believed that the results of further quantitative studies will show that the dominants of a sere can be arranged in a linear sequence from the pioneer stage to the climax. At the same time, it seems completely established that this sequence falls naturally into stages or associes, characterized by dominants of the same life-form and similar requirements. As a consequence, it becomes possible to use the dominants or consocies of a sere to indicate the successive small steps in the changing water-content from the initial bare or denuded area to the climax, while the associes indicate the stages of longer duration which are characterized by a certain set of water conditions. In the prisere, such conditions and their indicators have some relative permanence, but in the subsere the successional movement is much more rapid and the stages sometimes obscured. In both cases, however, the basic principle holds that a complete series of indicators marks the changes of water-content from an originally hydrophytic or xerophytic bare area to the relatively mesophytic forest climax. The exact value of each community or dominant as an indicator must await more general quantitative study, but the approximate values that can be assigned them at present are of genuine service in forest problems.

Light indicators.—The general principles which underlie light indicators in the forest have been discussed at some length in Chapter XIII. The tolerance of western dominants has been indicated by Zon and Graves (1911: 21), Sudworth (1908), Larsen (1916:437), and others. In a study of the tolerance of New England forest trees, Burns (1914, 1916) concludes that tolerance "really expresses not a light relationship, but the total relationship of a tree to all the factors of its habitat." While the results of Fricke (1904) and Burns have shown that competition for water must be taken into account in studies of tolerance, light is still to be regarded as playing the paramount rôle. Burns's further conclusion that light readings in the forest are of little value is often not in accord with extensive experience in making and utilizing such readings in ecological studies. On the contrary, one of the chief difficulties in the correlation of edaphic communities with their habitats is the absence of measurements of light intensity. Where these have been made with care and in large number through several years, as in the Pike's Peak region of the Rocky Mountains, they have proved invaluable in the study of reproduction, development, and plant indicators, as well as in that of leaf adaptation and photosynthetic efficiency. Measurements of light intensity in the forests of the West have been made by Clements (1905, 1910), E. S. Clements (1905), Pearson (Zon and Graves, 1911:46), and Bates (1917:233). Studies of the quality of forest light have been carried on for several years by means of a portable spectrophotometer (Clements, 1918:291), but the detailed results have not yet been published.

Site indicators.—The term site, like forest type, has a wide range of meaning among foresters. While it is regularly employed to denote the habitat, it is applied to all possible divisions of the latter. This is understandable,

since this is the present ecological practice in the case of habitat. But just as it has proved necessary to distinguish habitats of different character and various degree, so it is desirable to recognize several categories of site. Climax and seral habitats or sites are fundamentally different, though they are often found side by side. The habitat of one consociation differs from that of another of the same association, and mixed areas of the two show subordinate differences. Finally, the same consociation exhibits marked variations in growth and density, each corresponding to smaller differences of the factor-complex.

In practice, the forester has emphasized two of the several categories of sites. The first is the consociation habitat or the site occupied by a dominant, and the second the minor sites marked by significant differences in the growth or density of a particular dominant. The more specialized use of the word has been in the latter connection (Roth, 1916: 3; 1918: 749; Watson, 1917: 552; Bates, 1918: 383). As a matter of fact, the two types are developmentally connected, the growth sites, commonly designated as I, II, III, and IV, representing a sequence of minor habitats within that of the dominant consociation, such as *Pinus ponderosa, Pseudotsuga,* etc. The recognition of growth sites is chiefly important in connection with yield tables and working plans. In planting operations, consociation sites must first be determined, and then growth sites may be employed to ascertain the most promising areas.

Growth as an indicator.—As stated in a previous chapter, the presence of a dominant furnishes one set of indications, and its growth, another. The latter naturally affords a more sensitive scale of measurement, and hence indicates the effective differences of the habitat in terms of timber production. It is obvious that total growth is the most complete indicator, as Bates has insisted (1918: 383), though it is equally clear that height-growth or even width-growth may be used with much success. Since readiness and convenience are essential in the practical use of indicators, height-growth has received the most attention at the hands of those interested in the classification of sites. The whole question of site indicators as well as the advantages of height-growth in this connection has been well stated by Frothingham (1918: 755):

"Any method of determining forest sites must employ an indicator, whether this be the probable ultimate forest ('climax type'), the height-growth of one or more species present, the current annual volume increment of a fully stocked pure stand, some herb or shrub typical of a locality, or merely the composition of the existing stand. Similar sites are then to be recognized either by the identification of similar indicators or by determining the similarity of the physical-site factors. These may be measured in precise terms or simply estimated. Precise measurements appeal to the investigator. Accepting the permanent type as an indicator, for example, it would only remain to learn quantitatively the physical factors determining it. These physical factors wherever found interacting in precisely the same amounts will always produce, in time, barring accident or design, precisely the same form of forest. The plan of classification based on physical factors appeals to the investigator because it is truly fundamental. The apparent difficulties in deciding what is the permanent type in the isolation and measurement of the several physical factors, etc., may not be so formidable, after all, and the

work may be simplified by the discovery that only one or two of the factors are of particular significance. In many large regions, the permanent forest type is strikingly apparent. In other places it remains exceedingly obscure. Even where plainly evident, subdivisions with reference to yield are a necessity from considerations of future as well as present management. This subdivision of permanent forest types or of any other kind of types can be effected by the use of an indicator. Indicator plants, volume growth, and height-growth are means to this end. Under certain circumstances the use of indicator plants may prove very useful, as experiments by Korstian and others indicate.

"The use of the current annual increment as a means of determining site involves the double difficulty of securing a basis and of applying the measure of the site, when found, to the identification of similar site conditions elsewhere. As an exact indicator it may prove the last word in refining previous site determinations in localities where it can be employed, but as a general method, suitable for immediate use, it fails to meet the requirements of simplicity and widespread utility previously set forth. The utility of height—one of the functions of volume, but far less unwieldy as an index—ought to be plainly evident to everyone as the logical immediate basis for subdivision. Height-growth, as a matter of fact, appeals in two ways: First, as an immediate means of classifying forest sites in general, and second, as a guide and a short cut in arriving at a possible future classification of sites on a physical or permanent type basis.

"In conclusion, the principle of height-growth as a guide to site has the following features:

"1. It is simple, natural, easily understood, and easily applied in the field.

"2. It is independent of the determination of physical sites producing definite permanent forms of forest; but the two are not antagonistic; both are 'indicators' and both demand equally a determination, more or less refined, of the physical factors of site.

"3. The sites determined by height-growth are species sites, not permanent-type sites; hence they are useful with reference to short-lived intolerant and long-lived tolerant species growing in the same stand.

"4. By adopting one or more index species (intolerant species of wide occurrence on a variety of sites) the height-growth of other species can be gauged, their relative value in each site can be determined, and this value can be expressed by naming the site in terms of the growth of each species present, and, by analogy, of other species which do not happen to be present.

"5. It affords a means of comparing the growth of all American species on the basis of the soil and climate to which each is best suited, as well as in less favorable sites.

"6. It permits a ready comparison (*a*) between even-aged second-growth stands in widely different regions, thereby avoiding such inconsistencies as those to be found in the published yield tables for the same species in different States; and (*b*) between second-growth and old-growth stands in the same or different regions.

"7. Since height-growth is sensitive to interferences in the natural life of the stand (fire, culling, changes in density, etc.) care and judgment are necessary in the choice of trees to serve as the index; but except for very precise site determinations, the method, if used with ordinary caution, will undoubtedly prove serviceable for the majority of wild-woods conditions as well as for even-aged stands.

"8. As the knowledge of the laws of growth of our species increases, the refinement of site determination by height-growth can be increased."

The correlation of height-growth with rainfall and other factors has been made by Pearson (1918: 688) for *Pinus ponderosa* in Arizona:

"Western yellow pine in northern Arizona makes its height-growth during the period of lowest precipitation in the year. During this period of high activity, the trees are dependent almost entirely upon moisture stored in the soil during the preceding winter and spring. Normally the great bulk, and in some years all of this moisture, is stored during the winter months, December to March. When winter precipitation constitutes the sole supply, height-growth in young saplings is apt to be small. If winter precipitation is supplemented by 2 inches or more in April and May, a pronounced stimulus to height-growth results. It may be stated as a general rule for the sites covered by this study, that 2 inches or more of precipitation between April 1 and May 31 is several times as effective as the same amount in excess of the normal precipitation between December 1 and March 31. Factors reflecting atmospheric moisture conditions, including evaporation, wind movement, relative humidity, cloudiness, and length of rainless period, from April 1 to June 30, show a close, though not entirely consistent, relation to height-growth. Temperature on the sites studied appears to be important only in so far as it affects moisture conditions. Since the increase in temperature results in increased water consumption, height-growth, if, as is usually the case, there is a shortage of moisture, varies inversely with temperature. Observations indicate that where moisture is abundant, height-growth increases directly with temperature. Complete records of soil moisture, if available, would probably show even a closer relation to height-growth than does precipitation."

It is highly probable that water-content is the factor that exerts the primary control upon height-growth, and width-growth also. However, it seems practically certain that the competition for water and food between the growing points and the cambium ring determines that height-growth shall largely precede width-growth during each year as well as during the life history of the individual (Mitchell, 1918). The studies of Brewster (1918: 869) indicate that "the height-growth of larch seedlings does vary in accordance with variations in weather conditions from year to year, and that the most favorable conditions for rapid height-growth are produced in the North Idaho region by a combination of temperatures somewhat above the average, coupled with a high percentage of clear days, with an average amount of precipitation evenly distributed in the form of good rains at intervals of four to ten days preceded and followed by lighter showers." The greater rainfall, lower temperature, and greater cloudiness of northern Idaho in comparison with northern Arizona readily explain the relatively greater importance of temperature and light in height-growth, as well as the difference in the seasonal occurrence. This must be expected for the various climax associations, for which the task of correlation is primarily one of discovering the limiting factor by the measurement of the habitat complex.

In the determination and classification of sites, as well as in their discussion, it will conduce to clearness to recognize that this is almost wholly a matter of applying the indicator method. While the word site appears to refer to the physical conditions, it does so only in so far as these are indicated by the presence or growth of the species concerned. And while it is felt that the species affords a better measure than instruments do, such a measure is one of actual growth and not one of the controlling or limiting

factors. Hence, it must be recognized that height-growth indicates habitat only in a general way, and that its specific indications apply only to the productiveness of the area in terms of a particular tree crop.

Burn indicators.—It is a general rule that subclimax dominants serve as the typical indicators of forest burns. This is in conformity with the principle that almost any consocies and many socies of the subsere may indicate fire as well as other similar disturbances, the particular initial stage depending upon the degree of disturbance or the frequency of its repetition. The universal occurrence of tree and shrub consocies as burn indicators is explained by the fact that fire not only produces areas temporarily free from the competition of the climax species, but also characterized by conditions favorable to less exacting species. Their characteristic dominance is chiefly due to the rapidity and completeness with which they occupy the ground, as a consequence of excessive seed production, the opening of cones by fire, or the ability to produce root-sprouts. The conifers rely almost wholly upon the first two methods and chiefly the second, while the deciduous trees depend mainly upon root-sprouts. Among trees, the three types are represented respectively by *Pseudotsuga* and *Larix,* such pines as *Pinus contorta* and *attenuata,* and by aspen, birch, and alder. The scrub indicators owe their character almost wholly to root-sprouting, reinforced more or less by seed production and mobility.

The burn subsere consists of the usual stages of annual and perennial herbs, grasses, shrubs, and trees. However, the number and distinctness of the stages and the duration of the subsere depend chiefly upon the severity of the burn. In the mose severe burns the initial community often consists largely or wholly of mosses and liverworts, *Bryum, Funaria,* and *Marchantia,* and is followed by one of annuals, and this by one of perennials. The species, and to a less extent the genera, of these vary with the climax association, but such species as *Agrostis hiemalis, Epilobium spicatum, Achillea millefolium,* and *Pteris aquilina* are more or less universal. The development of a grass stage is less regular, since its place is often taken by scrub when the root-sprouting shrubs are abundant. The scrub is normally replaced by aspen, birch, or alder, and these may yield to a subclimax forest, such as that of lodgepole pine, or be replaced directly by the climax. It is obvious that fire may sweep through the scrub, aspen, or lodgepole communities, and initiate new subseres, producing an intricate pattern of seres and communities. In the great majority of cases, the succession is more or less telescoped, and often completely so. The root-sprouting ability of the shrubs and aspen and the release of the seeds inclosed in cones or buried in the duff enable the shrubs and trees to begin development the first year, at the same time that the herbs appear. In such cases practically all the dominants appear at once, but the development still exhibits many of the features of succession. The stages, though brief, give character to the area in the normal sequence and each disappears in turn as the competition of the next one becomes too great for it.

For the reasons just given, the herbs are relatively unimportant indicators in complete burns, though they are characteristic in the case of light ground fires. The burn subsere is characterized almost wholly by scrub, deciduous woodland, or subclimax forest, not only because of the duration of the latter, but also because repeated fires tend to make them relatively permanent. On

account of differences of distribution as well as the general similarity in requirements, the three types rarely occur in the same subsere. Two, however, are frequent, aspen and lodgepole being the most common. The rule is that the dominant with the greatest requirements is the subclimax. This is in accord with the occurrence of lodepole as the characteristic burn community in the northern Rocky Mountains, aspen in the southern, and scrub in the Southwest and in California. As burn indicators, they have several features in common, in spite of their differences in life-form. They not only indicate the possibility of reestablishing the climax by preventing fire in some cases or by planting in others where the original climax dominants have disappeared. But they also make it clear that artificial means and fire especially must be resorted to in areas where it is desirable to maintain the subclimax as a relatively permanent type (plate 41).

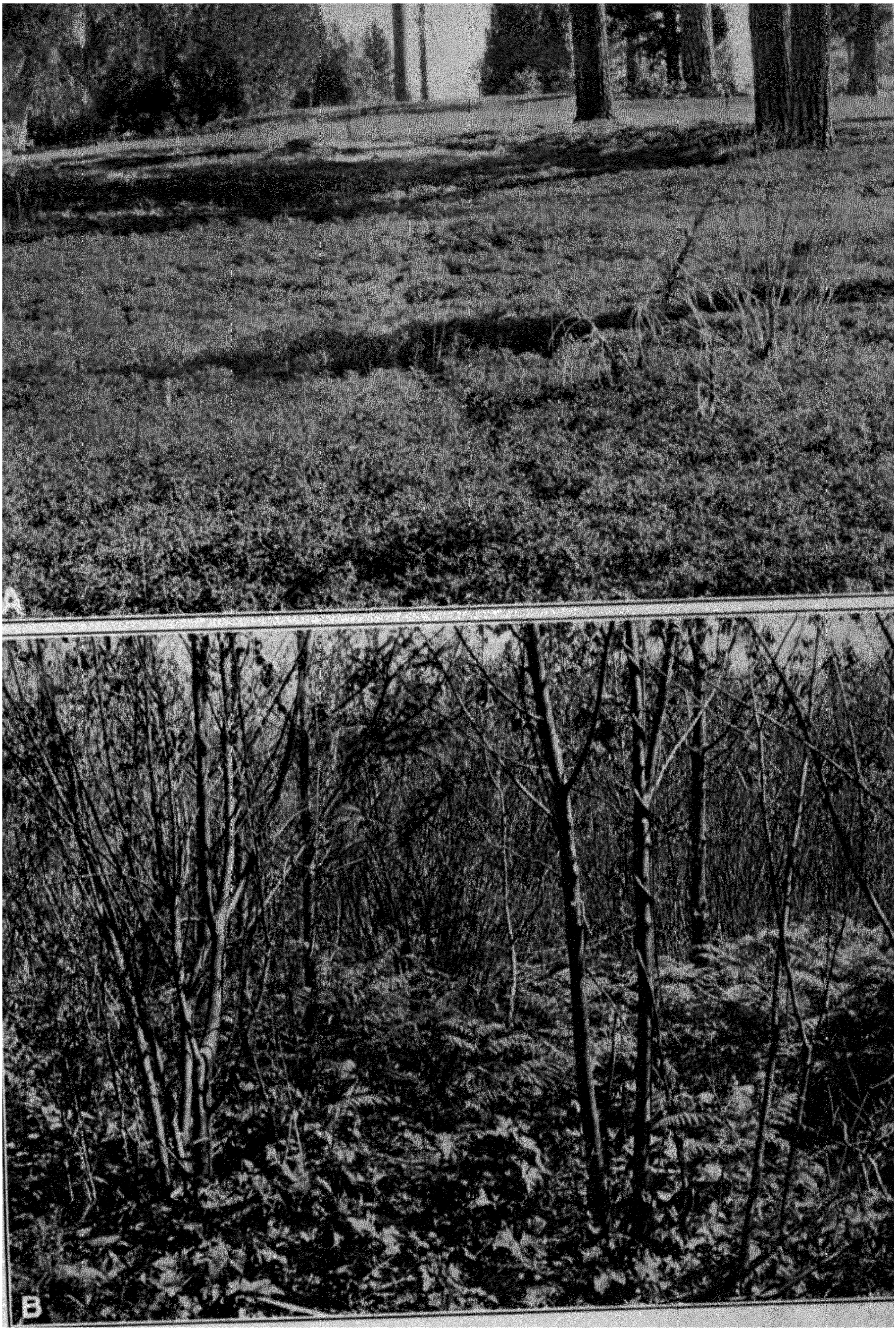
The importance of burn subclimaxes has been emphasized by Clements (1910:56) in the case of the lodgepole pine:

"The lodgepole forest is the key to the silvicultural treatment of the forests of the eastern Rocky Mountains, especially in Colorado and Wyoming. Its position in a zone between Douglas fir and yellow pine below, and Engelmann spruce and alpine fir above gives the forester a peculiar advantage. Its enormous seed-production, the power of the seeds to remain viable in the cones for years, its preference for soils of moderate water-content, the dependence of reproduction upon sunlight, and its rapid growth are all points of the greatest value in enabling the forester to accomplish his results. And it is by means of fire properly developed into a silviculutral method that the forester will be able to extend or restrict lodgepole reproduction and lodgepole forests at will."

The relation of aspen to lodgepole in burn subseres and its rôle as a temporary type have been dealt with in the same study (20, 47). The significance of aspen as a burn subclimax and its importance as a temporary type have been discussed by Pearson (1914:249), Sampson (1916:86), and Baker (1918: 294, 389). In the Northwest where *Pseudotsuga* forms a remarkable permanent subclimax in burns of enormous extent, Hofmann (1917:23) has reached the following conclusions:

"The study of burns and cut-over areas in the Douglas-fir region of the Pacific Northwest has brought out the following facts: The distance to which seed trees are capable of restocking the ground is limited to from 150 to 300 feet. They can not, therefore, account for the restocking of the large burned areas. The irregular dense stands of young growth are due to seed stored in the forest floor or in cones. This seed retains its viability through the fire and is responsible for the dense reproduction that springs up after the first fire. The even-aged stands of reproduction immediately following a fire, regardless of location of remaining seed-trees, the irregular alternation of dense stands of reproduction with grass areas, and the failure of reproduction on areas burned over by a second fire before the stand reaches seeding age, or by consuming all of the duff and precluding any possibility of seed remaining after the fire, all point to the seed stored in the duff as the principal source of seed responsible for the restocking.

"Since the seed must be produced by the stand before it is destroyed, the age at which the different species begin to produce seed is of the utmost importance. It varies greatly, and this variation alone is often the controlling factor in determining the composition of the second growth. For example,



A. *Chamaebatia foliolosa* indicating fire in pine forest, Yosemite National Park, California.

B. *Pteris* and *Rubus* indicating a recent burn, following one marked by *Arbutus-Prunus* associes, *Pseudotsuga* forest, Eugene, Oregon.

when western white pine, Douglas-fir, and knobcone pine (*Pinus attenuata*) appear in a mixed stand which is destroyed by fire, all of these species may again appear in the next stand; but if this second growth is destroyed by fire when it is from 10 to 12 years old, the next stand will consist principally, if not wholly, of knobcone pine. The knobcone pine begins producing seed when it is 6 years old and is producing good crops of seed at 10 years, while the white pine and Douglas fir bear only occasional cones at ages under 12 years. Therefore the knobcone pine is the only species which has any seed present to produce a forest stand following the second fire. Instances of such types are the knobcone pine types on the Siskiyou National Forest."

Scrub communities are regularly indicators of fire where they are in contact with forest. In fact, sagebrush appears to be a fire subclimax in the piñon-cedar woodland, as well as in the southern portion of the Coastal chaparral. Chaparral, however, is the typical scrub indicator of fire in woodland and forest. This is as true of the subclimax chaparral along the eastern edge of the grassland climax as it is of the Petran and Coastal associations. The most characteristic development of chaparral as a burn indicator is found in the montane forest in California, where the scrub persists as a more or less complete forest layer (p. 213; cf. Mitchell, 1919:39; Foster, 1912:212). Chaparral owes its importance as a fire indicator to its remarkable ability to form root-sprouts, and hence the form of the dominant shrubs is itself a response to fire. Fire in chaparral leads to a short subsere, in which the herbaceous stages persist for only a few years before the new shoots overtop them. Repeated fires may produce a subclimax characterized by *Eriodictyum,* or by *Artemisia, Salvia,* and *Eriogonum.* In the region of its contact with woodland and forest, chaparral is an indicator of forest burns, and consequently is subclimax. This is true in both associations, but is more marked in the Sierran, perhaps because of its greater massiveness. Munns (1919:9) has assumed that all of the latter is a temporary type due to fire, but this certainly seems not to be true of the regions with 12 inches or less of rainfall. This assumption is largely due to a misconception of what constitutes the test of a climax. Both of the tests used, the successful planting of trees and the existence of scattered trees and tree stands, would prove the grassland climax to be a temporary one. The critical processes in the establishment of a forest are seed-production, dissemination, and ecesis, and artificial planting is powerless to throw light upon the outcome of these. Further studies of the chaparral formation during the past three years have confirmed the view expressed in 1916 (Plant Succession, 180) that it constitutes a real climax, though portions of it are undoubtedly subclimax. This view is supported by the conclusions of Cooper (1919), who has made an intensive study of the California chaparral upon the instrumental and successional basis.

Grazing indicators.—With reference to the forest itself, only those grazing indicators are of importance that indicate overgrazing, and hence actual or potential damage to the reproduction. The presence of the usual overgrazing indicators would serve this purpose, but these are usually accompanied by evidences of damage to the seedling as well. However, while abundant evidence of this nature denotes overgrazing, it is still a question as to just when this becomes critical in the reproduction of the forest. In fact, it is clear that the critical degree of overgrazing depends much upon the nature of the community, time of year, age of the seedlings, and other factors. Much

light has been thrown upon the problem by three careful studies in the national forests (plate 42).

Hill (1917:23) has reached the following conclusions with reference to the damage done to seedlings in the yellow-pine forests of northern Arizona:

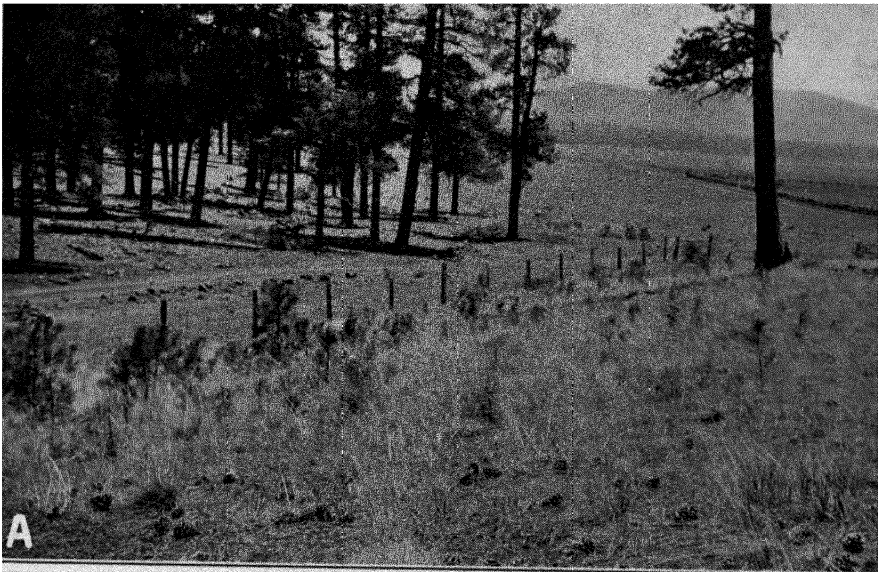
"Of 8,945 trees of a size subject to grazing, observed over a period of three years, 1,493 or 16.7 per cent were severely damaged each year and 1,222 or 16.1 per cent were moderately damaged. The most injured are the seedlings, 21 per cent of which are seriously damaged. The damage gradually decreases with an increase in the size of the trees. Trees above 4.5 feet in height are free from damage by browsing. The greatest amount of damage occurs during the latter half of June and the first part of July, or when the effects of the spring dry period are most pronounced. Under normal conditions of grazing, cattle and horses do an inconsiderable amount of damage to reproduction. Sheep under the same conditions may be responsible for severe injury to 11 per cent of the total stand. On overgrazed areas all classes of stock are apt to damage small trees severely. Cattle and horses may damage about 10 per cent of all reproduction. Where sheep are grazed along with them, however, at least 35 per cent of the total stand may be severely damaged. The amount of palatable feed available during the grazing season, and especially during June and July, has an important bearing on the amount of damage that grazing will cause to reproduction."

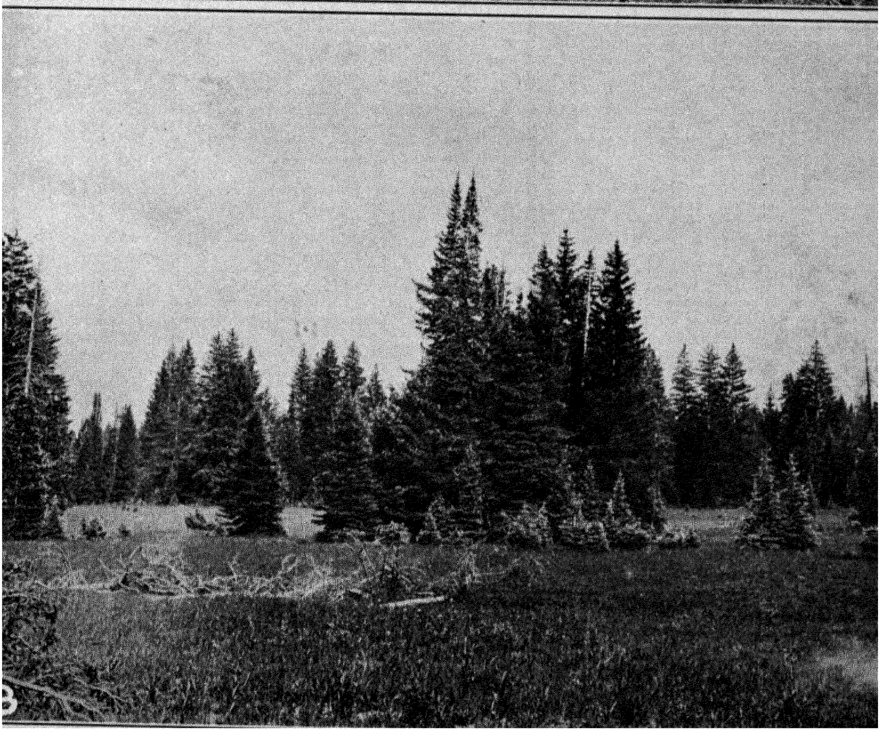
Sparhawk (1918) has shown that the damage to seedlings more than a year old is negligible in the yellow-pine forests of central Idaho, while the mortality of seedlings less than a year old averages 20 per cent. He states that, on the whole—

"More than three times as many seedlings were killed by other causes as were killed by sheep grazing, and five times as many were injured. As a general rule, the range should be grazed just enough to remove the greater part of the palatable forage. Extensive browsing of the least palatable species or of conifer reproduction is the best evidence that the area is being grazed too closely not only for the good of the range, but also for the best interest of the stock. Steep slopes with loose soil, particularly where the seedlings are less than a foot and a half high, and reproducing burns, clear-cut areas, or plantations with seedlings up to 5 or 10 years old, depending on the site, should be grazed rather lightly, especially in the first part of the season or during a wet period. In many instances it will be desirable to eliminate grazing entirely from plantations or other areas of seedlings less than three years old. During a dry season spots where danger of fire is greatest may be grazed as closely as possible."

Sampson (1919:25) has summarized the results of his study of the effect of grazing upon aspen reproduction as follows:

"The leafage, young twigs, and branches of the reproduction are browsed with varying degrees of relish by both cattle and sheep. Over 90 per cent of the damage inflicted by stock is chargeable to browsing, the injury due to trampling, rubbing, and similar causes being negligible. Sheep are responsible for severe damage to the reproduction, both as it occurs in standing timber and on clear cuttings, regardless of the variety and supply of choice forage. Cattle cause some damage, but the extent of injury is usually slight, except where the lands are overgrazed or where the animals are inclined to congregate for more or less lengthy periods. The injury and mortality chargeable to the presence of live stock is roughly proportional to the closeness with which the lands are grazed. Observations covering a 50-year period in standing timber





A. Pine reproduction in an exclosure, Fort Valley Experiment Station, Flagstaff, Arizona.
B. Reproduction cycles of *Picea engelmanni*, Uncompahgre Plateau, Colorado.

on sheep range showed that 27.2 per cent of the reproduction was either injured or killed on lightly grazed plots, 31.8 per cent on moderately grazed areas, and 65 per cent on heavily grazed plots. During 1915 and 1916 the average percentage of injured and killed sprouts by cattle browsing was 1.6 2.4, and 26.8 on lightly, moderately, and heavily grazed plots, respectively. On clear-cut lands, where the reproduction is conspicuous and the stand even, the annual mortality due to sheep grazing is exceedingly heavy. As a rule three years of successive sheep grazing on such lands results in the destruction of the entire stand."

Cycle indicators.—Trees, and shrubs also, may serve as indicators of climatic cycles by virtue of their growth, seed-production, or reproduction. In addition, there appears to be a certain correlation between the frequence and intensity of forest fires and the dry and wet phases of the cycle. The growth of trees as recorded in the annual rings is the classic material for the studies of Douglas, Huntington, and Kapteyn upon climatic cycles. The width of the ring indicates the varying rainfall of different years so clearly that Douglass (1919) has found it possible to cross-identify rings from trees grown many hundreds of miles apart. He has also found that the yellow pines of central Arizona often indicate two growing periods in one year by the formation of a double ring, and Shreve (1917:706) states that this appears to be regularly the case with trees at 6,000 feet in the Santa Catalina Mountains. It seems almost certain that height-growth and volume will likewise show cycle correlations, and this is suggested by Pearson's results in the study of the relation of height-growth to spring precipitation in northern Arizona (p. 426). The suggestion that seed-production is related to climatic cycles is based upon its well-known periodicity (Zon and Tillotson, 1911:133), as well as upon the fundamental fact that as a growth response it is controlled primarily by water and temperature. It seems probable that the seed-production cycle of pines especially is a response to the interaction of the 11-year cycle and the excess-deficit cycle of 2 to 3 years.

Reproduction reflects more or less faithfully the variations in rainfall during the 2 to 3 year, the 11-year, and the 22-year cycles. This correlation is clearly seen in the case of woodland and montane forest, especially at the lower limit, but it is naturally less evident in climaxes with a higher rainfall. It is most striking where woodland or forest is in contact with a community of lower water requirements, such as grassland, sagebrush, or chaparral, and shows less in the reproduction on the forest floor. All the cases of tree savannah and "natural parks" so far investigated warrant the working hypothesis that reproduction in such areas is cyclic and corresponds as a rule to the 11-year cycle, though minor variations conform to the 2 to 3 year cycle. There is also considerable evidence that the success or failure of planting operations has often been determined by their accidental coincidence with the wet or dry phases of the 11-year cycle, while it is obvious that in the future planting should be carried out with reference to the phases of the 2 to 3 year and 11-year cycles.

PLANTING INDICATORS.

Kinds.—Indicators of sites for planting are of two kinds: (1) those that indicate the former presence of forest; (2) those that suggest the possibility of developing forest in grassland or scrub areas. The first are indicators of

reforestation, the second of afforestation. The obvious indicators of reforestation are relict survivors, or trunks and stumps. Less obvious but equally conclusive are charred fragments or pieces of charcoal in the soil. In those cases where there is no direct evidence of the original forest, the desired clues are readily afforded by indicator communities which bear a definite relation to the forest. Such are seral and especially subclimax communities which exhibit a successional relation to the forest climax, and societies of shrubs or herbs which formed layers in it. While the latter are frequent in burns and clearings, they are usually accompanied by tree relicts which furnish more direct evidence. In some cases, however, they are the sole indicators of the former existence of forest in a particular spot. Subclimaxes are by all odds the best indicator communities of forest climaxes, since they show that the habitat has reached the condition in which the climax dominants can thrive. The earlier communities of a subsere have nearly the same value, since the habitat undergoes relatively slight change. In the case of a prisere, only the grass and scrub stages indicate that the slow reaction upon the originally bare area has reached a point in which remaining changes may be compensated by planting operations. Afforestation indicators are savannah, chaparral, or grassland of tall-grasses, in which the water requirements are sufficiently near those of trees that the gap may be bridged by planting methods, and especially by making use of the increased rainfall of the wet phase of the climatic cycle.

Furthermore, the indicators of sites for planting or sowing serve also to indicate the preferred species. In the case of reforestation, the general rule is that these are the climax trees that were in possession, but reasons of management may make it desirable to employ a subclimax dominant, such as lodgepole pine. Similarly, the growth-form best adapted for planting in a region is the one developed by that region, as the Forest Service has repeatedly demonstrated at its experiment stations. In the case of afforestation, the indications as to species must be derived from tree communities somewhere in contact with the grassland or scrub, as from pine in the case of the sandhills of Nebraska, from the indications of an intermediate community, such as scrub, or from the comparative study of habitats.

Prerequisites for planting and sowing.—The critical part played by rodents and by competition in natural reproduction was recognized more than a decade ago (Clements, 1910). Extensive tests of sowing in many national forests by the Forest Service has shown that destruction or control of the rodents is imperative (Tillotson, 1917:50). In fact, it seems evident that for practically all regions rodents are the most serious enemies of both natural and artificial reproduction, and that they should be systematically and permanently cleared out of all areas in which reproduction is important. Competition is a process which is less readily controlled on a larger scale. Competition for water is much more decisive as a rule than for light, the latter usually becoming critical only in dense scrub or similar communities. The disturbance of the soil involved in planting seedlings or in sowing by the seed-spot method usually suffices to reduce water competition sufficiently, except in a grass sod. The latter is usually encountered in clearings and in grassland associations in which afforestation is the method to be employed. In climax grassland, where the annual rainfall is less than 25 inches, the grasses use all

of the water-content during the drier portions of the season. As a consequence seedlings or transplants have little chance of survival unless the sod is destroyed about them, or unless planting is done during a period of unusual rainfall. As a desirable precaution under all conditions, the competition of the grass cover should be decreased by such treatment as the density of the sod and the nature of the soil will permit (Bates and Pierce, 1913:43). By far the most important practice in this connection, however, is the utilization of climatic and seasonal cycles to evade serious drought during the first few years (Hofmann, 1919).

Use of climatic cycles.—The critical importance of wet and dry periods for planting plans is strikingly shown by the variations in rainfall for the two areas in which afforestation has been tried on a large scale. The lowest rainfall at Valentine, on the northern edge of the sandhill region of Nebraska, was 10 inches in 1894; the highest was 28 inches in 1905. The lowest rainfall at Garden City, in the sandhill region of Kansas, was 9 inches in 1893; the highest was 29 inches in 1898. In both cases the rainfall of the wettest year was practically 3 times that of the driest, and the wettest and driest years departed practically 10 inches from the normal. A somewhat similar condition is shown at higher altitudes, where most of the reforestation planting and sowing is done. The base of Long's Peak, altitude 8,700 feet, shows a variation from 14 to 30 inches, while Pike's Peak, altitude 14,100 feet, exhibits a range of 9 to 44 inches. In all of these, the minimum rainfall occurred at the maximum of the 11-year sun-spot cycle, while the maximum rainfall either occurred at the sun-spot minimum or was related to it through the excess-deficit cycle of 2 to 3 years. In planting operations, the minimum is to be avoided at all costs, and this can be done almost certainly by utilizing the date of the maximum of the sun-spot cycle of 11 years. It is almost as important to anticipate a period of several wet years. The correspondence of the wet phase with the sun-spot minimum is not so good as that of the dry phase with the maximum, but it is sufficiently close in time and amount to make a great improvement over present methods. When the excess-deficit cycle is taken into account, the correspondence becomes so close as to warrant the assumption that planting can be planned in such a way as to avoid dry periods and to coincide with wet ones. For this purpose, however, it is necessary to determine the extremes of the climatic cycle in the particular region concerned.

Reforestation indicators.—The first definite proposal to use native plants as indicators of specific planting sites appears to have been made by Zon (1915):

"The selection of sites suitable for planting in a region which has been stripped of its natural timber is among the most perplexing problems. As long as there is a remnant of the virgin forest left, the latter may serve as a guide in selecting the species to plant on the given site.

"When, however, as is the case of the Ephraim Canyon and several other canyons on the Manti Forest, the original virgin timber has nearly disappeared altogether, both as the result of severe burns and grazing, and has been replaced by shrubs, herbaceous vegetation, and wide stretches of aspen cover extending over an area originally occupied by several forest types, the question of deciding what species to plant on a given site becomes very difficult

indeed. In such cases the shrubs and the herbaceous vegetation which occur throughout the canyon can be used to advantage as an indicator of the moisture content of the different sites and therefore for prognosticating the kind of timber the site can best support. The native shrubs and herbaceous vegetation, since they are not merely forerunners of the forest type that will eventually develop on a given site, but are also associates and are characteristic of different types as their typical undergrowth, are useful in deciding upon the species to plant. This is true not only where the original forest has entirely disappeared, but also on sites where there are still some traces of the original stand but which, because of the change in the physical condition of the site brought about by clear-cutting or burning, may better support a species which naturally grows at a somewhat lower elevation.

"For the purpose of artificial reforestation, Ephraim Canyon may be divided into five vegetation belts. The upper and lower limits of these vegetation belts vary, of course, on the southern and northern exposures; on the southern slopes the upper limits of each vegetation belt will extend to a higher elevation than on the northerly slopes, but wherever a certain vegetation is found it may be indicative of one or another natural timber belt, irrespective of the altitude or exposure. These five belts are as follows: (1) the lower timberless belt; (2) the yellow-pine belt; (3) the Douglas-fir belt; (4) the Engelmann-spruce belt; and (5) the upper timberless belt."

The indicators of the various zones are shown in figure 24.

Tillotson (1917:53) has pointed out the importance of indicators in the selection of planting sites (plate 43):

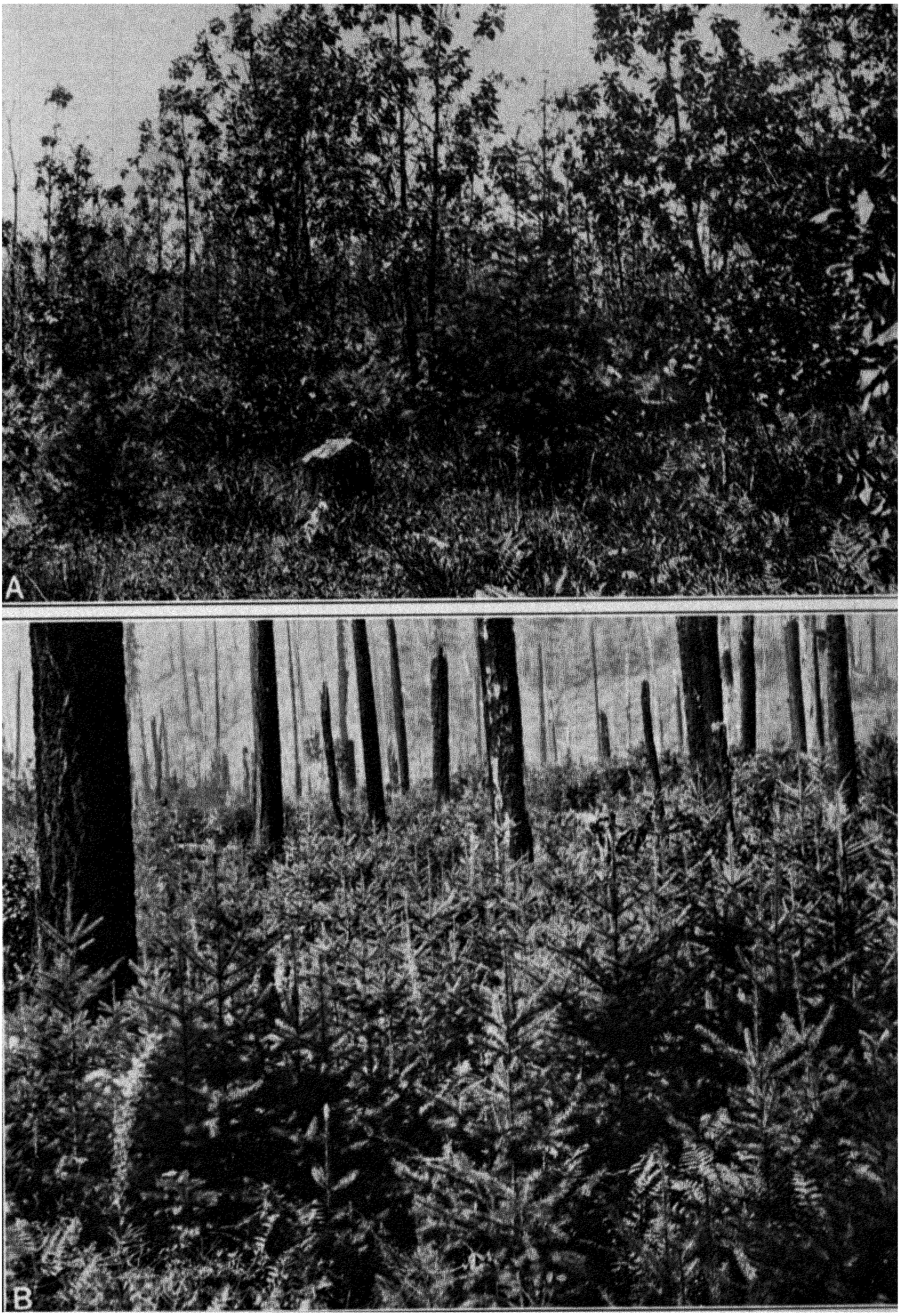
"The suitability of an area is very strongly indicated by the natural growth present. This is a pretty fair criterion of the quality of the site, and it points out the species which are most likely to succeed—either those which naturally occupy the area or others whose demands upon soil and climate are quite similar. A heavy growth of trees on similar adjacent sites will indicate that the area is quite probably suitable for sowing or planting; while a sparse growth of a drought-resistant species of tree on such sites will indicate that the area is only suited to reforesting with very drought-resistant species and that even then success will be uncertain."

He has also given a detailed summary of the planting indicators for the various regions and the most important species of the West. The nature and importance of his account may be gained from the following extract, which gives the indicators for Utah and southern Idaho:

"Western yellow pine in Utah: (1) Burned-over areas in the natural yellow-pine types; (2) areas covered with brush, mainly of oak, maple, and service berry; (3) areas covered with open stands of scrubby aspen; (4) sagebrush areas.

"Western yellow pine in southern Idaho: (1) Those sites producing yellow pine naturally; (2) brush areas within the limits of yellow-pine and adjoining stands of that species; (3) open grassy areas in the neighborhood of timber stands.

"Douglas fir: (1) Burns within the fir type; (2) sites covered with aspen of moderate density; (3) burns in the Engelmann spruce type; (4) areas covered with brush of oak, maple, service berry, cherry, and other deciduous species; (5) open grassland and mountain meadows. The planting of this species naturally centers mainly around the aspen type, particularly in Utah. The last two sites are not considered favorably for planting at present.



A. *Arbutus* as an indicator for reforestation, *Pseudotsuga* forest, Eugene, Oregon.
B. Burn reproduction of *Pseudotsuga* from seed in soil, Wind River Experiment Station, Washington.

"Englemann spruce: (1) Burned-over, non-restocking Engelmann spruce and balsam-fir cuttings; (2) the denser and better stands of aspen occurring at high altitudes; (3) lodgepole-pine burns.

"Lodgepole pine: (1) Lodgepole-pine burns which are non-restocking; (2) non-restocking Engelmann-spruce burns; (3) aspen-covered areas at higher altitudes. This species is not thought suitable for planting on brush areas nor on open grassy land where sheltering objects are missing."

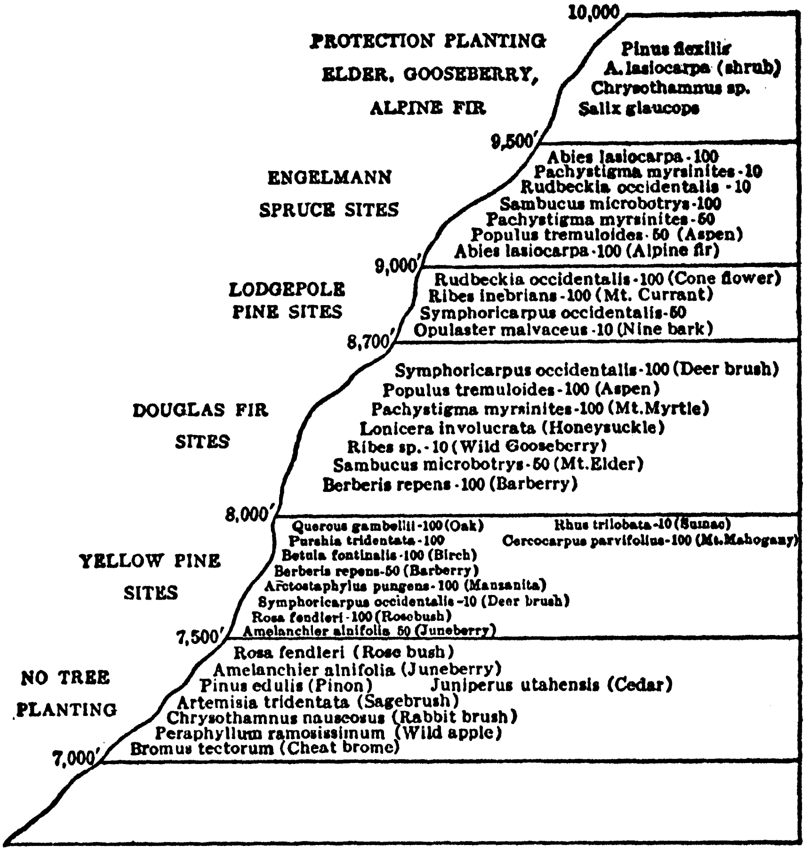


FIG. 24.—Indicators of planting sites in the various zones, Utah Experiment Station, Ephraim. After Zon.

Korstian (1917:281) has made use of the herbaceous and shrubby species in distinguishing between Sites I and II for yellow pine in the Datil National Forest in New Mexico.

"A perusal of the list shows marked differences in the individuality of the vegetation of the two sites. Site I is shown to produce such typical mesophytes as *Mnium* sp., *Agrostis hiemalis, Bromus polyanthus, Muhlenbergia wrightii, Populus tremuloides, Arenaria confusa, Cerastium longipedunculatum, Silene laciniata Aquilegia chrysantha, Thalictrum wrightii, Draba helleriana, Potentilla atrorubens, P. crinita, Rosa fendleri, Geranium richardsonii, Viola neomexicana, Amarella scopulorum, Gentiana bigelowii, Prunella vul-*

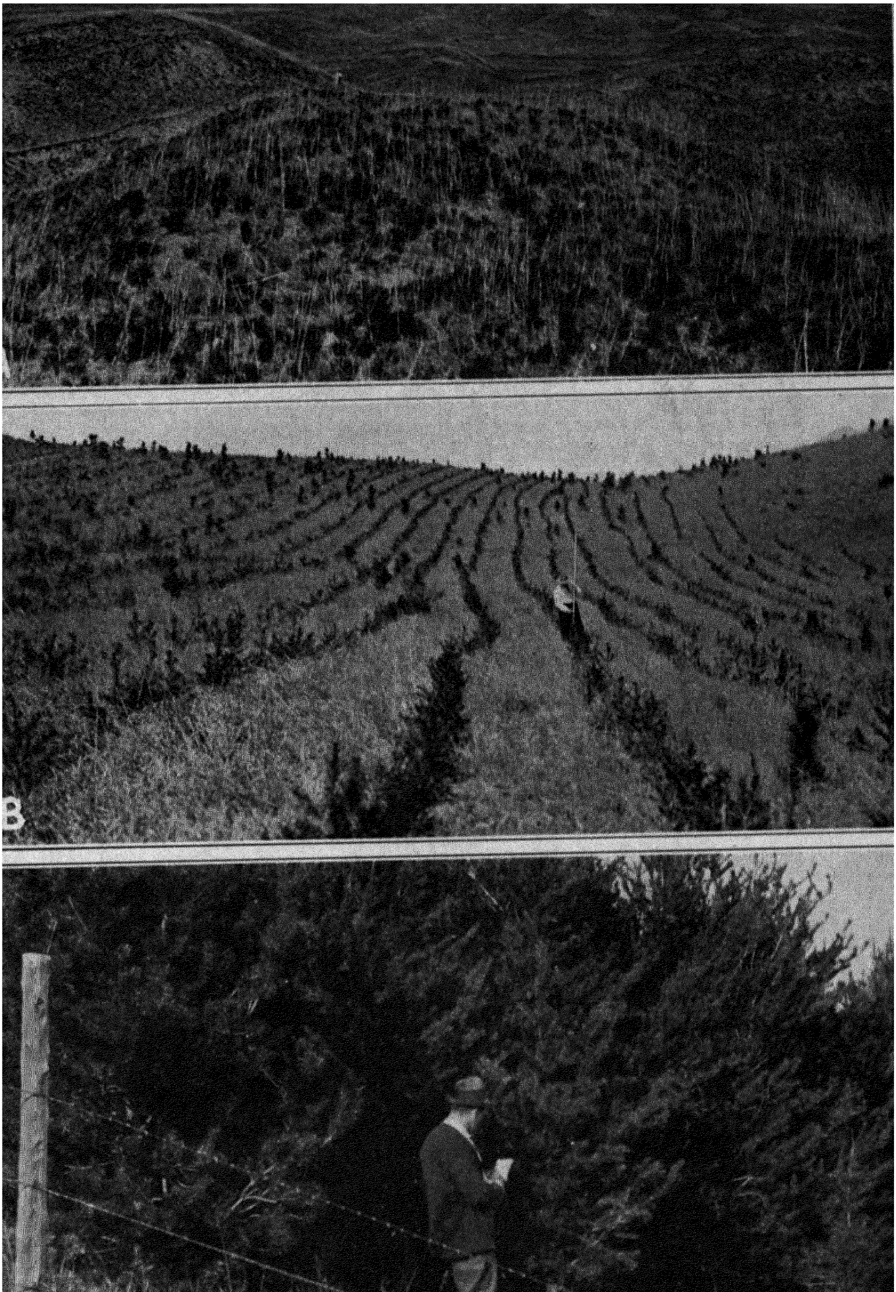
garis, Mimulus langsdorfii, Pentstemon virgatus, Campanula petiolata, and *Solidago neomexicana.* Site II bears such transitory species and xerophytes as *Poa rupicola, Commelina dianthifolia, Yucca* sp., *Quercus grisea, Portulaca oleracea, Heterothrix longifolia, Cercocarpus breviflorus* and *Hymenopappus radiatus.* The moss (*Mnium* sp.) was found only in cool, moist, and shaded situations, thereby indicating unusually favorable site conditions. The monkey flower (*Mimulus langsdorfii*) was the only plant which was confined to the proximity of water, indicating excessive soil moisture conditions.

"Practically all of the species listed as occurring entirely on Site II, which do not overlap on other sites, were found in hot, dry, and unshaded situations and might be regarded tentatively as indicators of poor western yellow-pine sites in the San Mateo Mountains. The mesophytes listed as possible Site I indicators were not found on poorer sites in this locality. However, it may be true that further detailed studies in the San Mateo Mountains might require a different listing of the vegetation than that here given. A number of the species listed as occurring on only one site are, to the writer's personal knowledge, known to occur on different sites in other parts of the Southwest. The vegetation on Site II was comparatively sparse and more open than on Site I where it was also more luxuriant and vigorous. Those species which were found to overlap on both sites normally made their optimum development on Site I. Approximately twice as many species were found on Site I as on Site II."

Afforestation indicators.—As already stated, the indicators of the possibility of forest production in grassland and scrub climaxes are either such extra-regional communities of trees as are found in savannah or in the fringing woods of river valleys, or such grasses and shrubs as indicate an approach to the water requirements of trees. As a matter of fact, practical afforestation has been confined chiefly to the sandhill regions of Nebraska and Kansas, in the first of which all four of these indicators have been present in some degree. Indeed, the success of planting in Nebraska and its failure in Kansas are related to the fact that these indicators were present in the one State and largely lacking in the other. While it is clear that no sharp line can be drawn between reforestation and afforestation, the latter is regarded as having to do only with those climaxes, grassland and scrub, in which trees occur at the margins or in valleys. While pine savannah and valley woodland were doubtless more extensive in the sandhills of Nebraska during the wet phases of some of the major climatic cycles of the present geological period, it is practically certain that this region has belonged to the grassland formation since the Miocene at least (plate 44).

Bessey (1887, 1895) was the first to point out the evidence which indicated that the sandhills of Nebraska could be forested, or reforested as he regarded it. This evidence consisted wholly of valley and canyon relicts of woodland, chiefly yellow pine. It was summarized as follows:

"There are many isolated canyons which contain trees; there are western as well as eastern trees and shrubs in these canyons; the yellow pine of the Rocky Mountains now grows with other trees upon the hills of Pine Ridge from the Wyoming line in Sioux County to the Dakota line in Sheridan County; the yellow pine is now to be found in the canyons of the Niobrara River and its tributaries as far east as the border of Holt County; it extended eastward along the North Platte River and Lodge Pole Creek to Deuel County until the pioneers destroyed it, forty or fifty years ago; it grew in considerable



A. *Andropogon-Calamovilfa* tall-grass postclimax in sandhills, indicating high chresard and the possibility of afforestation, Halsey, Nebraska.

B. Three-year-old plantation of jack-pine (*Pinus divaricata*) in sandhills, Halsey, Nebraska.

C. Jack-pines 10 years after transplanting, Halsey, Nebraska.

quantities in at least one station on the Republican River until destroyed by the early settlers; in the Loup Valley there are yellow pines on the South, Middle, and North Loup Rivers; logs and fragments of pine trees occur here and there in the sandhills."

Pool (1914:267) has considered in some detail the sandhill communities of shrubs which show the close approach to the water requirements of trees; among the most important of which are *Celtis*, *Prunus*, and *Salix*.

Bates and Pierce (1913:15) have discussed the sandhill shrubs in their general relation as indicators of forestation and of planting sites:

"Of the numerous woody undershrubs the yucca, or soap-weed (*Yucca glauca*), is probably the most striking plant of the sandhill region and is least abundant where the soil is the most stable and firm. Other shrubs, most of which are more or less gregarious and form clumps or mats on the ground, are the sandhill willow (*Salix humilis*), very common on north slopes and indicative of good moisture conditions, the redroot or New Jersey tea (*Ceanothus ovatus*), typical of sandy hilltops; the sand cherry (*Prunus besseyi*), found in almost any site, but especially in the loose sand around blow-outs; and the shoe-string bush (*Amorpha canescens*). Wolfberry (*Symphoricarpos occidentalis*), choke-cherry, and wild plum frequently form thickets on the slopes of pockets facing the southeast, where they are favored by the moisture from snowdrifts. The first-named seldom becomes more than 2½ feet high, the other two frequently 15 feet.

"From the standpoint of forestry one of the most important of the woody plants is the low bearberry or kinnikinnik (*Arctostaphylos uva-ursi*). While this grows in only a few limited localities, on moist north slopes, it is thought to be indicative of conditions favorable for western yellow pine, since it is an almost invariable associate of that tree in the Rocky Mountains.

"Typical of the stream valleys in both Kansas and Nebraska are the false indigo (*Amorpha fruticosa*), the buffalo berry, peach-leafed willow, sand-bar willow, wolfberry, plum, and chokeberry. The diamond willow, one of the Nebraska sandhills' most valuable small trees, is not found in Kansas. On the whole, shrubby growth is much more typical of the Nebraska than the Kansas sandhills, which usually have a heavy grass sod that does not permit the growth of shrubs."

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